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BEHAVIOURAL ECOLOGY AND CONSERVATION OF THE ANOSY MOUSE LEMUR (*MICROCEBUS TANOSI*)

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Thesis is submitted in partial fulfilment of the requirements of the award of Doctor of Philosophy, PhD.

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"Of Madagascar I can announce to naturalists that this is truly their promised land. Here nature seems to have created a special sanctuary whither she seems to have withdrawn to experiment with designs different from any she has created elsewhere. At every step, one meets more remarkable and marvellous forms of life"

- Philibert Commerson, *in a letter to Jérôme de Lalande, 1771.*

"Madagascar is a curious wonderland. It's an unrepeatable experiment, a set of animals and plants evolving in isolation for over 60 million years. We're still trying to unravel its mysteries."

- Sir David Attenborough, *BBC Broadcast on Madagascar, 2011.*

Cover photographs:

Front:

- View over the Sainte Luce flood plain between forest fragments S6 (Etazo) and S17 (Andranangy). (Photo by SHR).

Back:

- Multiple *Microcebus tanosi* concealed at a sleeping site in *Pandanus concretus*. (Photo by SHR).
- Twin crowned *Pandanus dauphinensis*. (Photo by SHR).
- Flowers of 'Vondroza' (*Sarcolaena multiflora*). (Photo by SHR).
- School children celebrating World Lemur Day in Ambandrika, 2015. (Photo by SHR).
- Aerial photography showing littoral forest fragmentation. (Photo by Daniel Wood).

Painted mural in the SEED Madagascar research camp, created by volunteers circa 2012.

An early representation of '*Microcebus rufus*'; referred to as '*Microcebus smithii*'. In *Handbook to the Primates* Vol.1; H. Ogg Forbes, 1894.

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ACKNOWLEDGEMENTS

This dissertation constitutes a major element of my work in the southeast of Madagascar, and the culmination of a period of six years working in the littoral forests of Sainte Luce. The completion of this study would not have been possible without the tremendous support of many people and institutions around the world. It is difficult to properly acknowledge the magnitude and value of each benefactor, and I inadequately address the most prominent here.

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THESIS ABSTRACT

Mouse lemurs are widely regarded as an ideal model taxa to study behavioural ecology, sociality and evolution in primates, however relatively few recognised forms have been studied to date. The principal aim of this work is to investigate the behavioural and ecological character of the Anosy mouse lemur (*Microcebus tanosi*) and to relate these new insights to species conservation in the littoral forests of Sainte Luce. The littoral forests of southeast Madagascar represent a distinct phytogeographic habitat, characterised by tremendous species richness and floristic diversity, however, they have been severely impacted by human activities over the past century. At the outset, very little ecological data was available for *M. tanosi*. Across five data chapters I investigate the species broad morphological flexibility, its ranging behaviour and social system, sleeping and nesting behaviours and its long-term demographic descriptives. I go on to contextualise the wider conservation challenges facing littoral biodiversity in Sainte Luce.

This study finds no evidence for sexual dimorphism but detects subtle morphological differences between isolated con-specific populations. *Microcebus tanosi* home ranges overlap substantially both inter and intra-sexually and are consistent with a dispersed social neighbourhood and promiscuous mating system, with males ranging over significantly larger areas than females. No evidence was found for the spatial monopolisation of receptive females by dominant males. Although *M. tanosi* is an apparent habitat generalist, utilising a wide variety of sleeping sites and tree species in the littoral forests, population density is low. Results indicate that predator avoidance best explains the patterns governing sleep site selection and highlights the key role of Pandanaceae species. This study demonstrates the importance of long-term population monitoring for nocturnal lemurs and highlights the critical relevance of local phenomena and forest management strategy for species conservation. Finally, this work provides several recommendations to counteract the observed decline in biodiversity in Sainte Luce.

CHAPTER 1

GENERAL INTRODUCTION

Cryptic speciation – The unveiling of Earth's hidden diversity

Recent insight into the natural phenomenon of cryptic diversity has led to a paradigm shift in our understanding of ecological complexity, with profound implications for a wide variety of fundamental human activities, including disease control, food production and biodiversity conservation (Wüster et al, 1997; Besansky, 1999; Molbo et al, 2003). A broad array of ecologically key species, previously considered as generalists, are increasingly now being recognised as cryptic complexes of specialist species with distinct ecological characters (Bickford et al, 2007). Cryptic diversity is now known to exist at all taxonomic levels throughout the tree of life and appears to be a fundamental aspect of the evolutionary process, characterising a wide variety of invertebrate and vertebrate taxa, including many primate groups (Bearder, 1999; Mayer and Helversen, 2001; Yoder et al, 2002; King et al, 2008; Nekaris and Munds, 2010; Dincă et al, 2011; Funk et al, 2012; Brasier et al, 2016). A cryptic species complex is defined as 'two or more distinct species that are erroneously classified (and therefore hidden) under one species name' (Bickford et al, 2007). The ubiquity of cryptic diversity throughout the natural world underscores the complexity of the evolutionary process and has opened up many new areas of research and revealed a multitude of taxa now requiring of further study.

It is now widely accepted that the process of speciation is not always accompanied by distinct and easily recognisable morphological change, and since many early species were described purely on this basis, the true number of biological species is believed to have previously been vastly underestimated (Bickford et al, 2007). In recent decades, a clearer image of the true scale of global species diversity has started to emerge, facilitated largely by the taxonomic renaissance made possible by advances in genetic techniques (Schindel and Miller, 2005; Kress and Erickson, 2012). Early scepticism related to the inflation of many cryptic taxa (Collar, 1997; Isaac et al, 2004; Mace, 2004; Tattersall, 2007; Markolf et al, 2011; Zachos et al, 2013) is gradually subsiding with the accruement of ever more powerful genetic analysis and as increasingly detailed ecological evidence is gathered. It is now apparent that morphological or phenotypic adaptation is similarly not always closely correlated with species boundaries (Heckman et al, 2006), but instead cryptic species may be distinctive in their use of non-visual mating signals or may experience some selective pressure that advances morphological stasis (Paterson, 1985; Bickford et al, 2007). Discreet differences in mating calls or pheromones between closely related species have been observed across a range of animal groups, including invertebrates

(Henry, 1994), amphibians (Narins, 1983), bats (Jones and Barlow, 2003), birds (Cicero, 1996) and primates (Hafen et al, 1998; Braune et al, 2008), forming the basis of prezygotic, reproductively isolating barriers that do not necessarily depend on obvious physical adaptation.

However, the true nature of global speciation patterns to some extent rests on the precise biological definition of what comprises a species unit. Whilst there are various interpretations (reviewed among others by de Queiroz, 1998, 1999, 2007; Mallet, 2007; Tattersall, 2007; Groves, 2011; Markolf et al, 2011; Wilmet et al, 2014), the 'Unified Species Concept' (de Queiroz, 1998; 1999; 2005) is now widely adopted by many biologists (Weisrock et al, 2010; Markolf et al, 2013). The concept incorporates elements of the 'Biological Species Concept' espoused by Ernst Mayr (1942) and defined as "groups of interbreeding natural populations that are reproductively isolated from other such groups" with common fundamental ideas outlined in other species definitions such as the 'Recognition Species Concept', which similarly identifies reproductive isolation and the possession of unique mate recognition systems as criteria (Paterson, 1978). Similarly, it combines aspects of both the 'Phylogenetic Species Concept' and the 'Genetic Species Concept', both of which require a lineage to demonstrate threshold genetic independence (Cracraft, 1983; Bradley et al, 2001). The PSC is defined as an irreducible group, diagnostically distinct from other groups, and who are each descended from a common ancestor (Cracraft, 1983; Groves, 2001; 2011). In contrast, the GSP is defined as a group of genetically compatible natural populations that can successfully interbreed (Bradley and Baker, 2001). Ultimately, the 'Unified Species Concept' combines the shared fundamental sentiment that 'species' represent a separately evolving lineage, but crucially views the secondary criteria of each concept or definition as additional lines of evidence (e.g. genetic threshold, phylogenetic distance or established isolating reproductive mechanism) for considering whether a lineage has truly separated. Whilst much debate still surrounds the number of species recognised under each definition, the 'unified species concept' has shifted the debate from a divisive philosophical disagreement to a methodological decision that facilitates better comparison (Wilmet et al, 2014).

The lemurs of Madagascar provide a particularly salient example of cryptic diversity and offer a window into the evolutionary mechanisms that drive and maintain species boundaries (Louis et al, 2006; Zaramody et al, 2006; Lei et al, 2014; Yoder et al, 2016b). However, the phenomena is not restricted to just lemuriform primates and is a characteristic shared with other strepsirrhine families (e.g. lorisidae and Galagidae) as well as tarsiers (Nekaris and Jaffe, 2007; Gursky-Doyen, 2010; Kappeler, 2012; Fleagle, 2013; Nekaris and Burrows, 2020). Over the past three decades, the number of recognised lemur species on Madagascar has increased dramatically, most notably within several nocturnal genera (Mittermeier et al, 2010). This link between cryptic diversity and nocturnality has long been recognised, with alternative forms of communication promoted over visual systems in the dark, resulting in

phenotypic stasis (Paterson, 1985; Bickford et al, 2007). Today, the Cheirogaleidae and Lepilemuridae represent conspicuously speciose primate families, characterised by cryptic diversity and that have been subject to frequent taxonomic investigation and revision (e.g. Rasoloarison et al, 2000; Yoder et al, 2000; Rumpler et al, 2001; Louis et al, 2006; 2006b; Radespiel et al, 2008; Rasoloarison et al, 2013; Hotaling et al, 2016;). Whilst the number of formally recognised *Lepilemur* species has exploded in recent times, increasing from just seven species in 1977, to 26 species today (Petter et al, 1977; Mittermeier et al, 2010; Wilmet et al, 2014), the most prominent genera in the Cheirogaleidae, *Microcebus*, has grown from just three recognised species to 26 and counting since 1993. Conversely, several other genera within the Cheirogaleidae (e.g. *Allocebus* and *Mirza*) have so far shown little or no evidence for widespread speciation (*Allocebus* remains monotypic), emphasising the non-uniform and genus level nature of the phenomenon (Bickford et al, 2007; Trontelj and Fišer, 2009). The evident skew in species richness within the Cheirogaleid genera supports the hypothesis that cladogenesis is more prevalent within certain groups (Bickford et al, 2007; Trontelj and Fišer, 2009). Although likely correlated with the distribution or range of the representative genera and linked to ecological requirements, the differentiated patterns of observed cryptic diversity remain largely unexplained. Beyond the genetic evidence, responsible for the determination of most lemur species in recent times, further work is now needed to establish reproductively isolating traits and other ecological and behavioural characteristics that both define and distinguish a diverging lineage from sibling species.

Evolution in a unique biodiversity hotspot – Madagascar

The unique biogeographic history of Madagascar makes it an ideal model system to explore the evolutionary mechanisms that drive speciation, micro-endemism and cryptic diversity. The island's ancient origins, isolation from other landmasses (Fooden, 1972; Reeves and de Wit, 2000; Jokat et al, 2003; Upchurch, 2008; de Wit, 2010) with very low rates of subsequent colonisation (Vences et al, 2009), it's tropical position and dynamic climate history (Gasse and Van Campo, 1997; Williamson et al, 1998; Burney et al, 2004; Crowley, 2010; Virah-Sawmy et al, 2010) have resulted in an unrivalled rich biodiversity (Myers et al, 2000). Furthermore, the island is divided into a number of distinct ecological zones (Dewar and Richard, 2007) which support unique floral and faunal assemblages (**Fig. 1**) (Burgess et al, 2004). Whilst Madagascar is truly still in a period of taxonomic discovery, with new species frequently described across many taxa, it is also now clear that Madagascar's megafaunal diversity was even grander in the recent past (Burney and MacPhee, 1988; Crowley, 2010). Regardless, species richness and endemism on the island is extraordinary (Myers et al, 2000), supporting an estimated 5% of the world's known species. 82% of vascular plant species are endemic (Callmander et al, 2011), along with 58% of bird species, 59% of freshwater fish, 96% of reptiles, 99% of amphibians

and 93% of mammals (including 100% of primates) (Ganzhorn et al, 2014). Furthermore, the endemic groups on the island are ancient, representing lineages with no close relatives elsewhere (Crottini et al, 2012).

To date, three broad biogeographical models have been developed to explain the unprecedented patterns of diversity across Madagascar, each encompassing the prominent phenomena of micro-endemism and aiming to address the underlying diversification mechanisms (Martin, 1972; Pastorini et al, 2003; Wilmé et al, 2006; Craul et al, 2009). The models largely focus on lemur distribution, and emphasise the role of major hydrographic systems, both historical and present, as key factors. River systems have similarly been invoked to explain the distribution of primates elsewhere in the Neotropics (Ayeres et al, 1992). The earliest model, and perhaps the simplest, postulates that large rivers form physical barriers which separate populations, preclude gene flow and ultimately result in allopatric speciation and the formation of distinct reproductively isolated lineages (Martin, 1972; Martin, 1995; Pastorini et al, 2003; Goodman and Ganzhorn, 2004). In this 'riverine barrier mechanism' scenario, river width, depth, temporal stability and the altitude of its source are crucial characteristics (Goodman et al, 2004; Vences et al, 2009). However, the long-term stability of many river systems is questionable (Ganzhorn et al, 2014). In contrast, the 'watershed' hypothesis contends that river basins act as the cradles for speciation, providing refuge during periods of climatic instability and protracted droughts (Wilmé et al, 2006; Wilmé and Callmander, 2006; Wilmé et al, 2012). The model invokes the historical climatic effects of the quaternary, a period when forest habitats experienced major contractions. Under this scenario, watersheds at low elevation become isolated as forest environments retreated along rivers, separated by expanses of arid and hostile habitat, resulting in vicariant divergence and high levels of micro-endemism (Goodman et al, 2004; Wilmé et al, 2006; Vences et al, 2009). In such refugia, species began to evolve new adaptations and become reproductively isolated. River systems with watersheds at high altitude may have allowed dispersal opportunities for some species able to traverse between river basins. The third model, a combination of the earlier two, identifying the important contributions of both river barriers and river basins in the evolutionary process, was developed to explain the distribution of *Lepilemur* species in northwestern Madagascar (Craul et al, 2007).

Although all three explanations are generally complementary, they crucially differ in the number of 'biogeographic zones', 'centres of endemism' or 'inter-river-systems', areas expected under each model to contain distinct communities. Whilst the 'large river model' hypothesis seems to explain the distribution and diversity of *Lepilemur* and *Microcebus* spp. in the northwest of Madagascar (Craul et al, 2007; Olivieri et al, 2007; Wilmet et al, 2014), the simple river barrier hypothesis has been used to explain the distribution of several other lemur genera (e.g. *Eulemur* and *Propithecus*) (Martin, 1972; Pastorini et al, 2003). However, it is now evident that large river systems can and do act as semi-permanent barriers for lemurs (Goodman et al, 2004; Craul et al, 2007; Vences et al, 2009). Yet, the

power of each model to explain specific patterns of diversity is likely complicated by other taxa specific factors, both ecological (e.g. dispersal capacity, altitudinal sensitivity) and environmental (e.g. local stochastic phenomena, rainfall patterns, habitat connectivity, ecozone type). Given the nature of diversity in Madagascar, and the relatively recent recognition of multiple cryptic genera, several areas still require further taxonomic investigation before accurate appraisal of true regional diversity can be made. As such, the distribution of diversity for some genera, in certain areas remains poorly understood. The recent discovery of a number of *Microcebus* forms in the extreme southeast (Rasoloarison et al, 2013; Hotaling et al, 2017), along with their seemingly specific distributional arrangements (Rakotondranary et al, 2011; Hapke et al, 2012), marks them out as being of specific interest from a biogeographical perspective. Particularly as the area spans a sharp ecotonal boundary and the region supports an array of forest habitat types (e.g. lowland humid forest, littoral forest, transitional forest and spiny thicket). It is against this complex ecological backdrop that important contextual elements of this study are set.

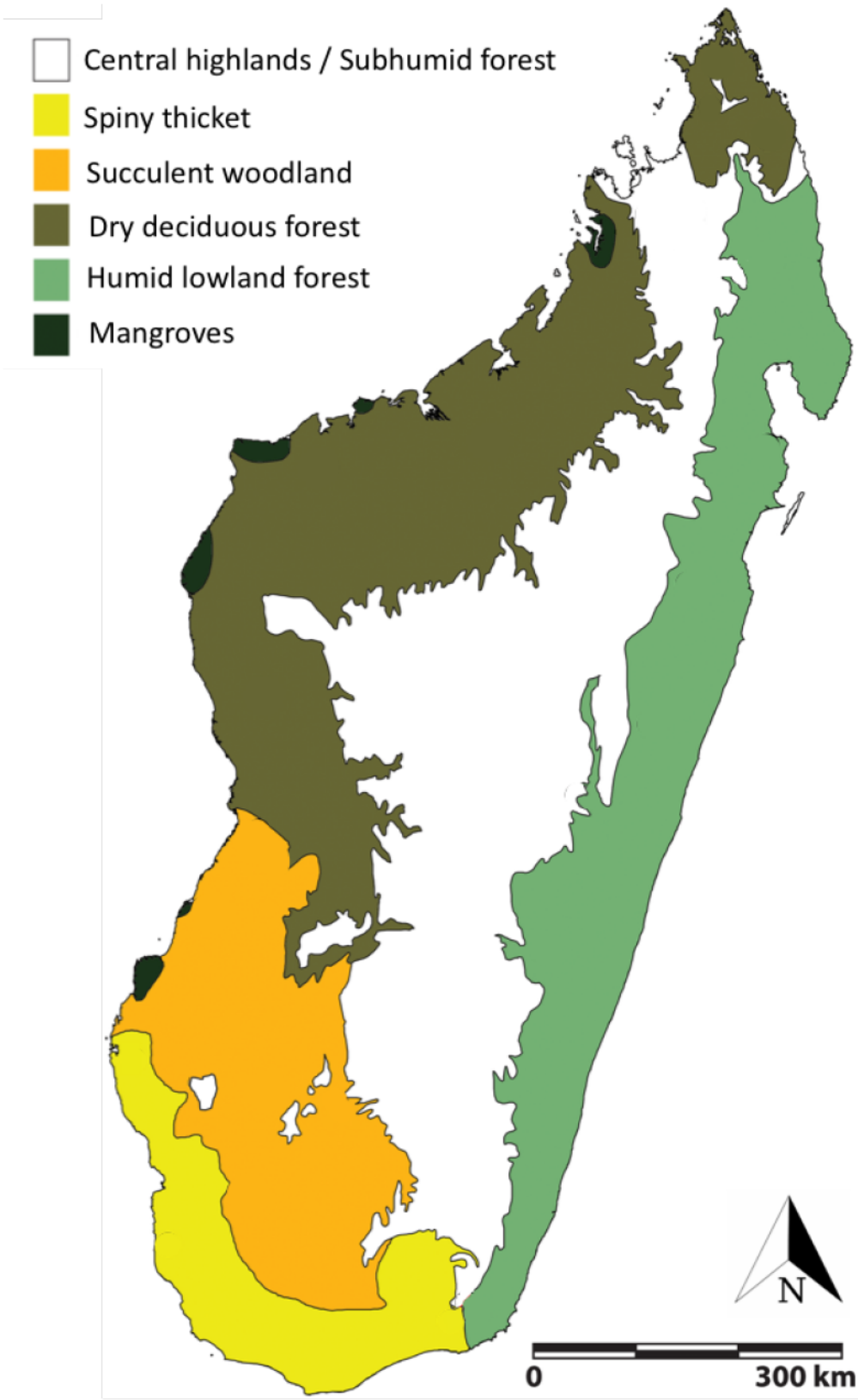

Figure 1 – The broad eco-regions of Madagascar, as described by Burgess et al, 2004. Each biome is characterised by highly specific flora and fauna. Figure adapted from Muldoon and Goodman, 2015.

Microcebus diversity in the extreme southeast of Madagascar

As a clade, mouse lemurs are broadly distributed throughout Madagascar and occupy virtually all forested areas, including habitats that are highly fragmented, limited in extent and badly degraded. As the number of studies increases and the coverage of Madagascar forests improves, it is becoming ever clearer that the mouse lemur radiation contains many microendemic species (Yoder et al, 2000; Louis et al, 2006; Radespiel et al, 2008; Sgarlata et al, 2019), with many under severe threat as a result of deforestation. Whilst species pairs are now known to exist in sympatry at several locations across Madagascar (Schmid and Kappeler, 1994; Zimmermann et al, 1998; Dammhahn and Kappeler, 2008; Radespiel et al, 2008; Sgarlata et al, 2019), the situation in the southeastern corner appears to be particularly intriguing, with at least five recognised species spatially clustered within some ca. 50km (**Figures 2+3**). Although species appear to be largely restricted to specific habitat types, the close proximity of many species in transition and connective habitats is of great interest (Hapke et al, 2011; Rakotondranary et al, 2011). Compellingly, the area appears to be the setting of a radiation event within the '*M. murinus'* phylogenetic cluster, with a number of sister species (*M. murinus*, *M, griseorufus*, *M. manitatra* and *M. ganzhorni*) all represented. In contrast, the region appears to be the mostly southerly extent of the *M. tanosi* distribution, corresponding with the edge of the Anosyenne and Vohimena mountain ranges and rainforest habitat. As such the area provides a unique opportunity to study the biological processes that are driving and maintaining diversification amongst the distinct lineages (Gligor et al, 2011; Hapke et al, 2011; Rakotondranary et al, 2011) yet at the outset of this study, many knowledge gaps remained with regards to species-specific behavioural ecology.

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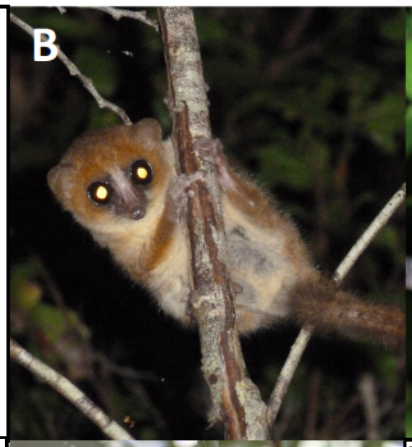

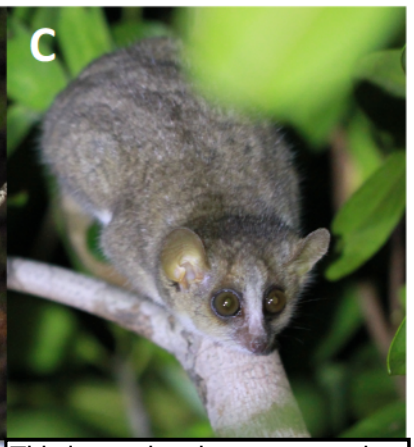

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Figure 2 – *Microcebus* spp. in the extreme southeast of Madagascar. **A**) *Microcebus manitatra*, **B**) *Microcebus tanosi*, **C**) *Microcebus ganzhorni*, **D**) *Microcebus* murinus, **E**) *Microcebus griseorufus*, **F**) *Microcebus* cf. *murinus*. Photographs: **A** Refaly Ernest, **B**, **C**+**E** Sam Hyde Roberts, **D** Jacques Rakotondranary and **F** Unknown.

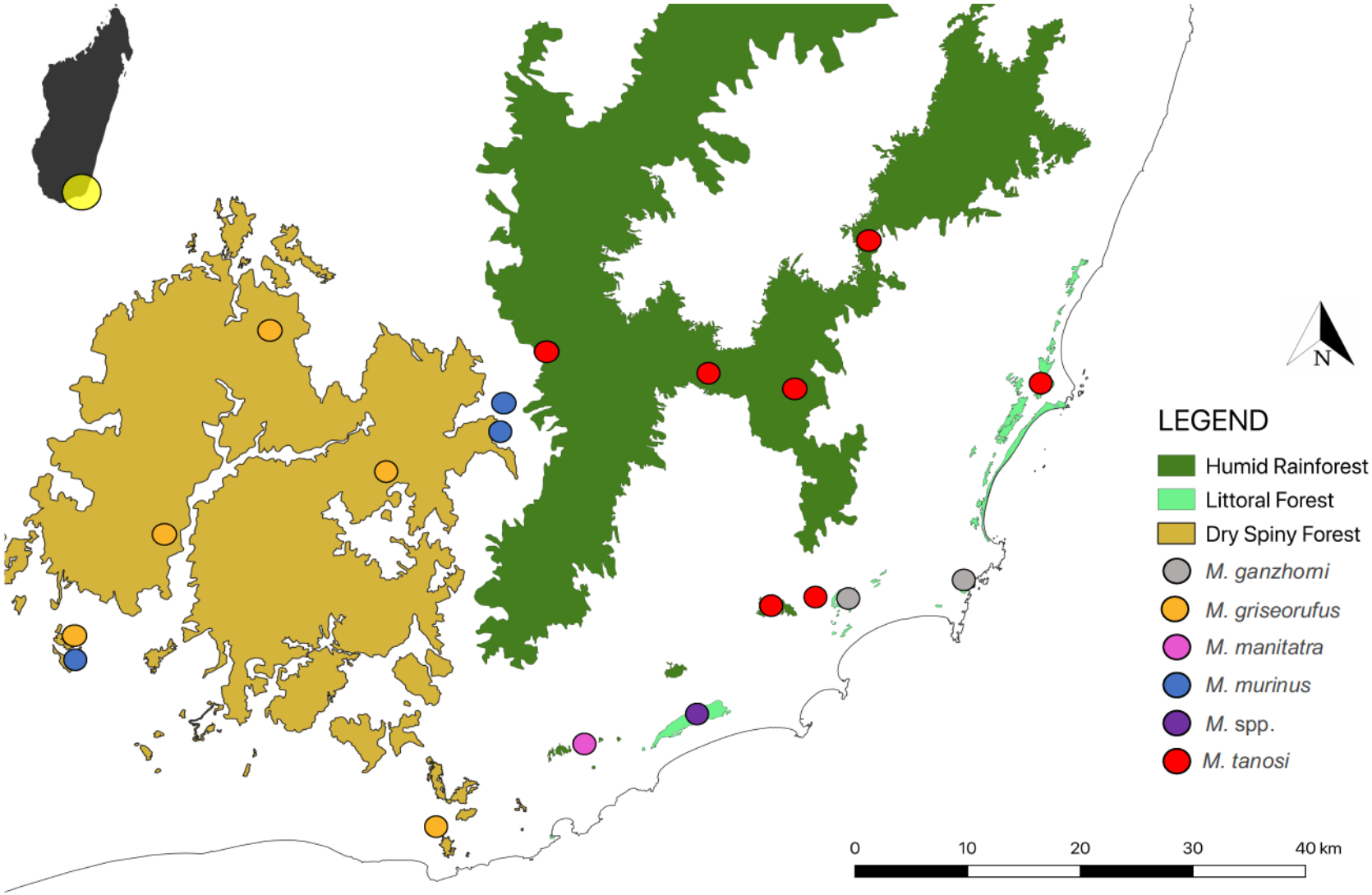

Figure 3 – The distribution of *Microcebus* spp. across the extreme southeast of Madagascar based on the current understanding.

The fragmentation of Madagascar's littoral forests

The littoral forests of Madagascar form a distinct phytogeographic habitat, a sub-type of eastern humid evergreen forest occurring on sandy coastal substrates (Ratsivalaka-Randriamanga, 1987; Lowry and Faber-Langendoen, 1991). Although a few large parcels still remain (e.g. Ambila Lemaitso, Ambondrobe, Foulepoint, Pointe à Larrée, Sainte Luce, Tampolo), Madagascar's littoral forests persist today as a series of small forest fragments that are patchily distributed along the eastern seaboard. These fragments extend from the northern tip of the island, between Antsiranana and Vohemar, to Tolagnaro in the south. However, it is a commonly held view that these littoral forest once formed a 1,600km continuous forest habitat along the eastern coastal fringe, and were further contiguous with the humid lowland evergreen forests inland (de Gouvenain and Silander, 2003; Consiglio et al, 2006). Conservative estimates suggest that just 10% of the original forest now remains (Du Puy and Moat, 1996; Consiglio et al, 2006; Moat and Smith, 2007). Despite their limited extent and degraded nature, the littoral forests support an extraordinary biodiversity, including approximately 13% of the island's total native flora, of which 25% is considered endemic (Dumetz, 1999; Moat and Smith, 2007).

Deforestation in eastern Madagascar is known to have been most rapid in areas with low topographic relief (Green and Sussman, 1990), with littoral forests among the country's most impacted formations (Schatz, 2000; Schatz et al., 2000). As a result, very little undisturbed littoral habitat remains and just a few patches exist within the current protected area network (Goodman et al, 2019). The contemporary loss of littoral forest is predominantly attributed to anthropogenic activities such as logging, resource extraction and fire (Goodman et al, 2019) and many of the remaining forests are still subject to heavy human pressure (Consiglio et al, 2006; Bollen and Donati, 2006). However, the true extent of pre-human forest cover on Madagascar is contested. In decades past, a dominant narrative has argued that Madagascar was originally entirely covered by woodlands, which were systematically exploited and severely reduced as human communities became increasingly significant (Perrier de la Bathie, 1921; Quémére et al, 2012). Given that evidence for some of the earliest known human settlements on Madagascar are from the southeast coast (Campbell, 1993), it could be expected that the littoral forests have been heavily exploited. However, recent studies suggest that past climatic fluctuations have had a profound impact on shaping current biomes well before the proposed arrival of humans (Dewar, 2003; Burney et al, 2004). Although there is uniform consensus that human activities dramatically transformed the landscape at about 1,000 y B.P. (Dewar et al, 2014; Goodman and Jungers, 2014; McConnell and Kull, 2014), the prehuman condition remains disputed (Yoder et al, 2016). Modern debate surrounding the original extent of woodland has centred on palynological and biogeographical records from various bioclimatic zones and the roles of Quaternary climate cycles and extent of intermediate habitats (Burney et al, 2003; Gasse and Van Campo, 2001; Matsumotot and Burney, 1994; Virah-Sawmy et al, 2010; Dewar et al, 2013; Burns et al, 2016; Vorontsova et al, 2016).

Vegetation reconstructions based on fossil pollen records in the southern littoral forests reveal a highly dynamic environmental history, with a shifting mosaic pattern of habitats types expanding and contracting in response to climatic changes (Virah-Sawmy, 2009). Analysis of substrate cores suggests that littoral forests in the region had been relatively stable for a protracted period of time (between ca. 5100 and 1000 years BP), but experienced substantial declines around ca. 950 years BP. This event coincides with widespread vegetation transformations and evidence of fire across the island (Virah-Sawmy, 2009), thought to have been triggered by pronounced arid conditions between 1200 and 700 years BP (Crowley, 2010; Virah-Sawmy et al, 2010; Bertoncini et al, 2017). Prior to this event, vegetation records across Madagascar show asynchronous responses to Holocene droughts, emphasizing the magnitude of the changes that occurred some 1000 years ago. Additionally, the position of the littoral forests means that they are substantially impacted by marine surges and changes in seal level. Furthermore, the hunting of megafauna (Burney, 1999; Crowley, 2010; Virah-Sawmy et al, 2010; Hansford et al, 2018; Godfrey et al, 2019) and important seed dispersing species may have impacted the functional integrity of littoral ecosystems around the same time as human communities became more significant.

Today open habitats dominate much of Madagascar, extending across approximately 80-84% of the lands surface (Olivieri et al, 2008), including the eastern coastal plains where littoral forest is thought to have once stood. Whilst the historical extent of littoral forest and the drivers leading to its reduction are contested, there is no doubt that modern deforestation is largely driven by human activities. In the littoral forests of the Tolagnaro region, forest cover declined by some 50% between 1950 and 2005 (Vincelette et al, 2007b) as a result of unsustainable human activities. Given the condition and limited distribution of littoral forests, and that they represent floristically distinct ecosystems, supporting endemic invertebrates and unique vertebrate assemblages (Du Puy and Moat, 1996; Ganzhorn et al, 2000; Schatz et al, 2000), they are widely considered a conservation priority in Madagascar.

Project genesis and justification

Given the broad taxonomic changes that have occurred across Madagascar since the mid 1990s, including revisions to numerous lemur species in the southeast (Pastorini et al, 2000; Zaramody et al, 2006; Lei et al, 2014; Rasoloarison et al, 2013), validating the identity of the nocturnal species in the littoral forests of Sainte Luce became a priority for local conservation and research works. As part of a small project undertaken whilst working for SEED Madagascar (see **Chapter 2**, **Project collaborators**), a small number of genetic samples were collected from each of the nocturnal lemur species present in Sainte Luce and barcoded to establish species/lineage identity. Initially, the work set

out only to confirm species identities and establish distributional parameters. Samples were exported and analysed by Dr. Christian Roos at the German Primate Center (DPZ). Whilst both *Avahi meridionalis* and *Cheirogaleus thomasi* were confirmed, *Microcebus* samples initially failed to match with any species registered on the genetic database GenBank. It is now known that a delay in uploading original voucher sequences, following the initial species description in 2013 (Rasoloarison et al, 2013), led to a failed BLAST match and the conclusion that the *Microcebus* form in Sainte Luce was potentially a candidate new species. The ambiguity surrounding the identity of the species generated by this initial result, and the prospect of yet a further cryptic species in the littoral forests was enough to prompt the immediate start of this study. During the early stages of the work however, further samples were collected and analysed, this time using nuclear DNA, and a match with *M. tanosi* was established, finally confirming the identity of the species in Sainte Luce and extending the known distribution of *M. tanosi* into the littoral forests.

Despite the initial confusion, at the outset of this study little ecological data was available for *M. tanosi* beyond scattered distributional and genetic work (Lewis Environmental Consultants, 1992b; Ganzhorn et al, 2008; Hapke et al, 2011; Rakotondranary et al, 2011) and only a small number of previous studies had investigated the species' demographics (Ganzhorn et al, 2008; Nguyen et al, 2013). Similarly, the species had not been formally assessed by the International Union for the Conservation of Nature (IUCN). Duly then, a thorough investigation into the behaviour, ecology and conservation of the species was necessary and the main broad aims of the thesis began to take shape. Research was largely focused within the littoral forests of Sainte Luce as the contextual background of the area was already well established and the research camp of collaborators SEED Madagascar is situated conveniently. Furthermore, Sainte Luce has been my research site since 2014 and a long-term and stable relationship with the community already existed. Combined this familiarity alleviated logistical and security challenges. Furthermore, given the heavily fragmented nature of the littoral forests and the continual pressures exerted by unsustainable community resource extraction and proposed mining activities (QMM, 2001; Temple et al, 2012), the lemur community required urgent attention.

The behavioural ecology of mouse lemurs

Mouse lemurs are widely distributed throughout Madagascar's forested habitats and as such exist across a wide range of environmental conditions (Mittermeier et al, 2010). They represent the smallest extant primates, with adults ranging from between just ~30g (*M. berthae*) to over ~70g (*M. murinus*), with *Microcebus berthae* recognised as the world's smallest primate species (Rowe and Myers, 2016). Yet despite the lack of obvious phenotypic separation between *Microcebus* forms, environmental variation

appears to have resulted in the expression of a range of behavioural adaptations across the genus. As with other nocturnal primate taxa (Nekaris and Burrows, 2020), social patterns in *Microcebus* are complex, ultimately determined by a combination of resource acquisition, territoriality, the reproductive synchronicity of females and predator avoidance (Altmann, 1990; Mitani et al, 1996; Dunbar, 2000; Kappeler, 2000; Eberle and Kappeler, 2002). At present, the available literature documenting mouse lemur sociality is limited in terms of the range of species it covers, partly since many species have only recently been recognised, but also due to the difficulties associated with the study of small, fast moving, arboreal and nocturnal species. However, despite the challenges, advances in technology (e.g. miniaturised telemetry devices, genetic tools) alongside the significant commitments made by the primatological community (wider sampling, radio-tracking, trapping studies) have given rise to an emergent body of evidence in support of a rich and diverse range of social behaviours and systems within the genus.

Reproductive seasonality is a key trait in governing social structure in many primate species and both mating and birthing patterns often coincide with times of peak food abundance (Koenig et al, 1997; Wright, 1999). Mouse lemurs are no exception; however, they do exhibit a suite of unusual reproductive characteristics. As a general rule, mouse lemurs reach sexual maturity within their first year of life, reproducing annually and within a highly constrained seasonal window, often correlated with bouts of prolonged torpor (Blanco, 2010; Blanco et al, 2015). Typically, mouse lemurs produce a single litter of between two to four offspring at the onset of the austral summer, however at least some species appear capable of exceptional physiological flexibility, adapting this schedule in unpredictable or harsh conditions. Female *M. murinus* have been recorded producing their first litter at just four months old and it is not uncommon for a single female to produce multiple litters in a year (Rina Evasoa, 2018). Studies on both wild and captive individuals demonstrate that reproductive activity is initiated by photoperiod but is also influenced by age. Given photoperiod is fundamentally linked to forest productivity (Wright, 1996; Bollen and Donati, 2005; Adole et al, 2019) and reproductive success depends ultimately on attaining sufficient resources, the connection between resource availability and the reproductive calendar is unsurprising.

Mouse lemurs were initially thought to exist as individuals within non-gregarious social systems, however, it is now clear that many species share well-developed social networks (Martin, 1972b; Kappeler, 1997; Atsalis, 2000; Radespiel, 2000; Weidt et al, 2004; Dammhahn and Kappeler, 2005). A significant proportion of interactions are displaced, with direct physical interactions replaced instead by vocalisations and olfactory cues (Eisenberg et al, 1972; Bearder, 1987; Martin, 1995; Hohenbrink et al, 2012; Kollikowski et al, 2019). At present, the available literature provides a broad consensus on the general model of social organisation and mating strategy that characterises mouse lemur systems, however, provides unambiguous evidence of clear species-specific variation. In general, all mouse

lemur species appear to be highly promiscuous, with males competing for mates within dispersed multi-male, multi-female communities (Fietz, 1999; Radespiel, 2000; Schmelting et al, 2000). All species studied to date exhibit considerable inter and intra-sexual home range overlap with the territories of males overlapping multiple females, although importantly, the degree of overlap varies between species, which is interpreted as a signal of disparate social organisation (Radespiel, 2000; Schwab and Ganzhorn, 2004; Dammhahn and Kappeler, 2005). Importantly however, the natural sex ratio of almost all mouse lemur species and populations is largely unknown and although ascertaining such information is extremely difficult, any skew towards either sex may have important downstream consequences for socio-ecological behaviours. Broadly however, such social characteristics indicate a tendency towards a 'scramble competition' mating system, whereby males compete indirectly with rivals for access to females (Wells, 1977; Schwagmeyer, 1988; Tew and MacDonald, 1994; Kappeler, 1997b). Given their dispersed social structure and pronounced reproductive synchronicity, males are unable to dominate access to large numbers of female individuals and so competition between males' manifests through elevated reproductive capacity, sperm competition and potentially an increased capacity for locating fertile females (Harcourt et al, 1981; Radespiel, 2000; Eberle, 2007).

An observed increase in the ranging area of male individuals in some species (e.g. *M. ganzhorni* and *M. murinus*), coincident with the reproductive season, is generally interpreted as a strategy to maximise reproductive success. However, this strategy is not shared by all species examined so far, with some studies finding the home range size of both sexes to be similar, at least during certain times of the year (*M. lehilahytsara*, *M. ravelobensis* and *M. sambiranensis*), and in the case of *M. griseorufus*, females occupy larger ranges than males (Pages-Feuillade, 1988; Radespiel, 2000; Randrianambinina, 2001; Weidt et al, 2004; Lahann, 2008; Génin, 2010; Jürges et al, 2012; Hending et al, 2017). However, in many cases, direct species comparisons are precluded by methodological constraints. Furthermore, these differentiated strategies are almost certainly modulated by local environmental conditions, and potentially even deeply rooted phylogenetic factors. Similar species level variation is also reported within the female reproductive strategies studied to date, with *M. murinus* females forming temporally stable matrilineal social core clusters (Radespiel et al, 2000) and female *M. ravelobensis* exhibiting philopatry (Radespiel et al, 2003), however neither phenomenon has been observed in *M. berthae* (Dammhahn and Kappeler, 2005). Furthermore, the malleability of social and mating systems in mouse lemurs has been further demonstrated in captive studies, where clear dominance hierarchies were established in both sexes in *M. murinus*, with dominant males siring an increased number of offspring and dominant females appearing to affect mate choice (Andrès et al, 2001). Although this has not been observed in any species in the wild, it again demonstrates the broad behavioural flexibility inherent in the genus.

Similarly, the degree to which species utilise their habitats, select sleeping sites and structure their social groups is known to vary amongst species (Radespiel et al, 1998; Schwab, 2000; Radespiel et al, 2003b; Weidt et al, 2004; Dammhahn and Kappeler, 2005). However, these expressions of social structure and organisation are again undoubtedly impacted by a multitude of factors tied to local conditions (e.g. climate, resource availability, population density, predation risk, reproductive phase, and habitat condition). Whilst there is a growing body of literature pertaining to the sleeping and nesting habits of wild mouse lemurs (Schmid, 1997; Radespiel et al, 2003b; Schwab and Ganzhorn, 2004; Weidt et al, 2004; Dammhahn and Kappeler, 2005; Genin, 2010; Luttermann et al, 2010; Hending et al, 2017), disentangling the complex web of inter-acting factors that govern these decisions is far from simple. Furthermore, given that the selection of a safe sleeping site is critical from a Darwinian perspective, and since mouse lemurs occupy an important trophic link in forest ecosystems across Madagascar, as prey species for a wide variety of vertebrate predators including birds, snakes and carnivores (Goodman et al, 1993; Karpanty and Wright, 2007), species-specific behaviours associated with sleeping site selection likely reflect fundamental strategies.

Likewise, in terms of diet, a considerable degree of variation exists between recognised species, although all are considered generalist omnivores. Again, the difficulties associated with studying the diets of wild mouse lemurs and the recent explosion in recognised forms has meant that relatively few species have been thoroughly studied in-depth (e.g. Hladik et al, 1980; Atsalis, 1999; Genin, 2001; Riemann et al, 2003; Dammhahn and Kappeler, 2008b; Radespiel et al, 2006). Small primates should theoretically concentrate on nutritionally dense food sources such as invertebrates (Hladik, 1979; Clutton-Brock and Harvey, 1983; Kay, 1984; Richard, 1985) to provide the readily digestible energy and protein necessary to fuel a hi-octane metabolism. However, the variety of energy dense food resources available to a particular species is clearly dictated by a habitat's climate and productivity. The diet of the limited species studied so far appears to contradict the established theory, containing large proportions of fruit and berries, supplemented by invertebrates, gums, insect secretions and small vertebrate prey (frogs, gecko's and small chameleons). In general, western and southern species (e.g. *M. berthae, M. griseorufus*, *M. ravelobensis* and *M. murinus*) occupying the drier forests appear to rely heavily on gums, plant exudates (Genin, 2001) and sugar rich insect secretions during the dry season (Corbin and Schmid, 1995), whilst rainforest species (e.g. *M. rufus*) appear to maintain a diet rich in fruits and berries throughout the year, and seemingly exclude gums (Atsalis, 1999). These broad trends again serve to emphasise the adaptability of the genus.

A further critical adaptation that appears to be expressed in a non-uniform manner across the genus is the capability to endure prolonged periods of cold or reduced resource availability. Whilst members of the Cheirogaleidae are the only known primate species to periodically hibernate, a number of mouse lemur species are similarly known to enter into bouts of daily torpor (periods of reduced metabolic

activity, typically lasting less than 24hours) and can even extend this to hypometabolic phases or hibernation (>24 hours) (Schülke and Ostner, 2007). Such adaptations are considered extreme, and individuals first undergo dietary preparation, periods of weight gain and fat storage. In additional to the species occupying more extreme environments (e.g. *M. griseorufus* in the southern spiny forests) rainforest species such as *M. rufus* are able to undergo periods of torpor and hibernation, as does *M. ganzhorni* in the southern littoral forests (Schülke and Ostner, 2007). Regardless of the complex triggers that initiate such exceptional strategies (Schülke and Ostner, 2007), it is supposed that all mouse lemur species have the capacity for undergoing bouts of torpor under specific environmental conditions.

Study aims and objectives

The principal aim of this study is to investigate the broad behavioural and ecological character of the Anosy mouse lemur (*M. tanosi*) and to relate these new insights to the species' conservation in the littoral forests of Sainte Luce. In additional to compiling all available data pertaining to the species (both published and unpublished), across five data chapters (**Chapters 3 - 7**) I investigate the broad morphological flexibility of *M. tanosi*, its ranging behaviour and social system, sleeping and nesting behaviours and its basic demographic descriptives in the littoral forest. With each chapter, new evidence is provided, and novel insights are gained. This study adds to the existing body of knowledge available for the genus, increasing our collective ability to examine broader trends across this highly cryptic and important primate radiation. I finally go on to contextualise the wider conservation challenges in the littoral forests of Sainte Luce, summarising the present situation (focusing on several key taxonomic groups) based on six years of study. Whilst the major component of this work focuses on the behavioural ecology of *M. tanosi*, its conservation in Sainte Luce is inextricably linked to the health of the littoral forest ecosystem and the complex relationships it shares with the wider ecological community.

In **Chapter 3**, I collate and synthesise all known biometric measurements available for the species (both published and unpublished), together with a novel data set collected across two field sites (Sainte Luce and Nahampoana Reserve). As well as providing a first robust biometric dataset, I explore the morphological flexibility of the species across its distributional range. Given that the species appears to exist across a variety of habitat types (littoral forest, lowland humid rainforest and even non-natural forest settings), assessing the effect of habitat type and its influence on specific biometric traits may highlight traits undergoing selection.

In **Chapter 4**, I describe the species' ranging behaviour and habitat use in the littoral forests of Sainte Luce during the reproductive season (October to February). Based on data obtained from a selection of

focal individuals, representing both sexes, I infer the social organisation and the general reproductive strategy of the species. By examining individual and inter-sexual variation in both range size and overlap, the chapter explores the fundamental nature of sex-specific social differences. Any observable difference in ranging behaviour is set within the theoretical framework of the socioecological model. This chapter adds to the growing body of knowledge available describing social behaviour in mouse lemurs and further facilitates a higher resolution inter-species comparison.

In **Chapter 5** I investigate and describe the sleeping and nesting behaviours of *M. tanosi*, based on a number of radio-collared individuals (both sexes) in the littoral forests of Sainte Luce. I examine the general habitat structures used by the species and investigate the ecological determinants that drive these critical behavioural decisions. I assess whether any fundamental differences exist between the sexes in terms of the general structures used, in the patterns of site fidelity and reuse and in social cohesion (stable sleeping groups). The chapter also examines the microhabitat characteristics of sleeping and nesting sites and explores the roles of predator avoidance and thermoregulation on site selection. This study again enhances our broader understanding of resting and nesting behaviour across the genus, helping to elucidate deeper environmental, ecological and phylogenetic based trends.

In **Chapter 6** I examine the long-term population dynamics of *M. tanosi* in the littoral forests of Sainte Luce, along with two other co-occurring nocturnal lemur species: *Avahi meridionalis* and *Cheirogaleus thomasi*. From the data I extract important descriptives (population size, population density, encounter rate etc.) and establish broad demographic trends over a period of eight years. This longitudinal study provides insight into natural population dynamics across three forest fragments, varying in both size and their protective status regimes. The study examines whether the community exhibits any species-specific trends and whether any observable patterns can be attributed to ecological factors such as diet, resource availability, or anthropological drivers such as habitat disturbance and forest management practices. The study contextualises the findings from a conservation perspective and assesses the need for practical conservation interventions.

In the final data chapter (**Chapter 7**), I evaluate the broader conservation status of the Sainte Luce littoral forests, primarily from a faunal perspective, based on six years of diverse and intensive field studies. By examining an array of vertebrate and invertebrate taxa (including lemurs, amphibians and reptiles, birds, small mammals, butterflies and dragonflies), the study highlights the main threats to local biodiversity, synthesises new taxonomic and conservation evidence, and examines the changes in faunal diversity and ecosystem structure over the past two decades. The chapter identifies key species within the community, assesses recent conservation focused interventions and provides recommendations for future actions. The chapter further proposes a list of 21 priority species that should form the basis for future biodiversity action planning.

CHAPTER 2

GENERAL METHODS

Study area (Sainte Luce Littoral Forests)

All of the ecological elements of this study were undertaken at a single locality, Sainte Luce, in the Anosy region in southeastern Madagascar. The littoral forests of Sainte Luce today form the northernmost part of a complex of littoral habitats in the extreme southeast, along with parcels Mandena and Petriky (**Fig. 4**). The commune of Sainte Luce (24°46.S; 047°10.E) is part of the wider Ambatoatsinanana area and at the last census (2019) supported 2,667 people (Berina. *Chef de' Fokontany*. pers comm), distributed amongst three small hamlets: Ambandrika (24°46'57.75" S, 47°10'23.99" E), Ampanasatomboky (24°46'48.4" S, 47°11'35.9" E) and Manafiafy (24°46'34.4" S, 47°11'53.5" E) with each supporting populations of 860, 607 and 1,200 respectively. The original fishing community (Manafiafy) was first established circa 1800 and today is also synonymous with Sainte Luce. The communities are situated within a series of 17 disconnected forest fragments (**Fig. 5**) covering approximately 1,550ha and spread along approximately 28km of the coastline. A description of each of the Sainte Luce littoral forest fragments is provided in **Table 1**. Early aerial photographs show that the forests have been in their current formation since at least the 1950s (Green and Sussman, 1990) but by 2005 had suffered extensive degradation through unsustainable human practices. Over the same period, forest cover across the wider Tôlañaro or Fort Dauphin region had been reduced by an estimated 50% (Vincelette et al, 2007c). Today, each of the Sainte Luce fragments are degraded to at least some extent and vary in condition, having been heavily exploited for natural resources for decades. Interestingly, using GIS tools this study has shown that overall forest cover has changed very little over the past decade (increasing very slightly from 1548ha to 1552ha now) but has declined since the beginning of the century (1771ha in 2000). However, the real deterioration of the forests has almost certainly taken place within the boundaries of the fragments and beneath the canopy. Examples of the Sainte Luce habitat are presented in **Figure 6**.

The remaining forest fragments in Sainte Luce are interspersed with small introduced plantations (*Acacia mangium, Eucalyptus* spp., *Grevillea robusta* and *Melaleuca quinquenervia*) and swamps, all embedded within a matrix of ericoid grassland (Ingram and Dawson, 2006; Virah-Sawmy et al. 2009). Formerly considered a heavily modified anthropogenic landscape, recent palynological studies indicate that these fire sensitive grasslands that separate the littoral forest fragments likely have a natural origin

and pre-date human colonisation (Virah-Sawmy et al. 2009; Virah-Sawmy et al. 2010). These relatively baron expanses are now subject to regular burning for cattle grazing and present a hostile environment for forest-dwelling organisms. The 'southern' littoral forests once thought to be contiguous with those in northeastern Madagascar, grow along a narrow coastal band of sand and alluvium and exist exclusively between the Vohimena Mountain's to the west and the Indian ocean to the east (de Gouvenain and Silander, 2003). The remaining southern littoral forests today all exist at less than 40m above sea level and are each within 3km of the coastline (Lowry and Faber-Langendoen, 1991; Consiglio et al. 2006; Ingram and Dawson, 2006). If littoral forest did once form a continuous band along the eastern coastline, it is estimated that only c.10% remains in the form of small fragments (Consiglio et al, 2006). Due to the high concentration of endemic plant and animal species supported by the littoral forests (Dumetz, 1999; Ganzhorn, 1998; Ramanamanjato, 2007, Watson, 2008), the remaining patches are widely regarded as national conservation priorities (Ganzhorn et al, 2001).

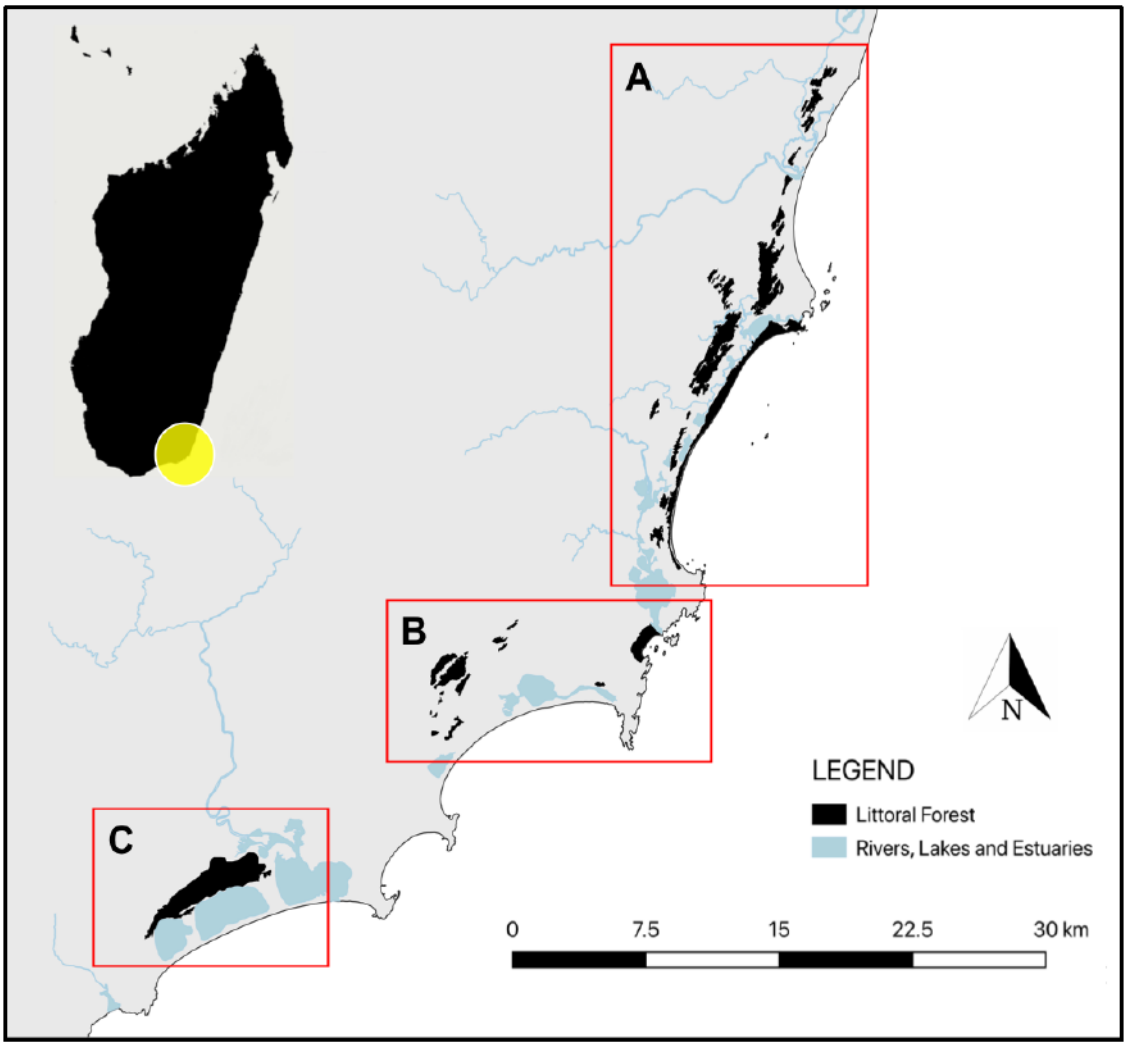

Figure 4 – The littoral forest blocks of southeast Madagascar; **A**) Sainte Luce, **B**) Mandena, **C**) Petriky.

Regardless of the initial extent of littoral forest in southeastern Madagascar, it is clear that these forests have had a highly dynamic history, heavily influenced by the marine environment (Abbott et al, 2006a, 2006b; Virah-Sawmy et al. 2009; Virah-Sawmy et al. 2010). There is no doubt the forests have been severely impacted by human communities since initial colonisation of the area, most likely during the 9th century (Rakotoarisoa, 1997; Wright and Rakotoarisoa, 1997). Today the capital of the Anosy region and closest major urban settlement to Sainte Luce, Tôlañaro or Fort Dauphin (25° 02'S 46°59'E), is some 50km to the south at the southern tip of the Vohimena mountain range. The city has a burgeoning population of roughly 70,000 people (Ministry of Statistics, Fort Dauphin October 2019), placing large and growing environmental demands on proximal natural resources (Vincelette et al, 2007c). The area continues to be one of the poorest and most isolated regions in Madagascar (Vincelette et al, 2007c). Over 80% of people living in the Anosy region live below the poverty line, the equivalent of 1USD each day (Vincelette et al, 2007c) and depend on a low-level commercial economy based around rice, sisal and lobster.

Despite growing demand and long-term resource extraction, the littoral forest fragments of Sainte Luce constitute some of the most intact examples of littoral forest habitat remaining in Madagascar, and support some of the highest species richness and floristic diversity on the entire island (Rabevohitra et al. 1996; Dumetz 1999; Ganzhorn et al, 2001; Bollen and Donati 2006; Consiglio et al, 2006). This forest habitat type is recognised as a distinct phytogeographic unit (Ratsivalaka-Randriamanga, 1987; Lowry and Faber-Langendoen, 1991) and is often defined as a dense and humid lowland forest with a relatively open or non-continuous canopy (Bollen and Donati, 2006; Consiglio et al, 2006). Average canopy height ranges between 10-15m in Sainte Luce (Goodman, 1997; Gouvenain and Silander, 2003b) with emergent trees occasionally reaching 20m and over. Most adult trees have a diameter (at breast height; DBH) between 30-40 cm (Dumetz, 1999) and generally less than 50cm in the largest trees (Goodman, 1997). Average monthly temperatures range from 26.9°C in January to 20.3°C in July (Temple et al, 2012). January is typically the wettest month and September the driest. Rainfall in the southeast is highly variable but averages between 1500–2400mm annually, with most rain concentrated between the months of November and April (Koechlin 1972; Goodman et al. 1997; Ingram and Dawson, 2006). Sainte Luce is known to receive a higher amount of precipitation than the other nearby littoral forests of Mandena and Petriky (Ganzhorn et al. 2007). Occasional cyclones occur between December and February.

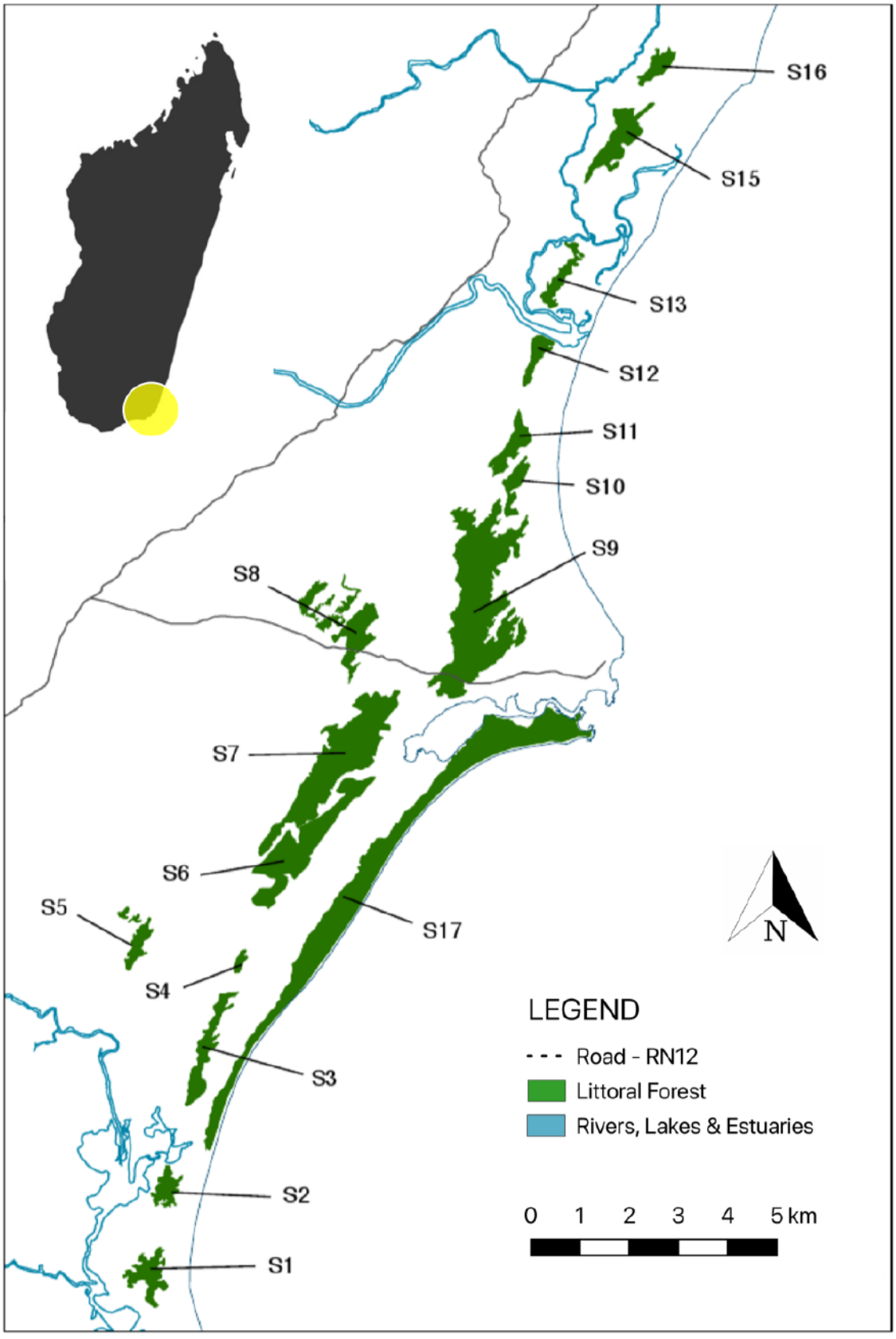

Figure 5 – The distribution of littoral forest fragments and major watercourses in Sainte Luce.

The forest fragments in Sainte Luce are generally now known by their shorthand, arbitrarily assigned numbers and the prefix 'S' for Sainte Luce by the locally invested mining operation run by QIT Madagascar Minerals (QMM), part of the RioTinto international mining consortium. The RioTinto QMM project proposes to exploit the ilmenite ore found in the mineralised littoral substrate and provide titanium dioxide to the worlds market (Temple et al, 2012). The project is currently underway in the more southernly series of littoral forests at Mandena and is set to sequentially operate in Sainte Luce and then Petriky in the coming decades. Previously, the project has set out an ambitious environmental agenda and committed to oversee a net positive impact on biodiversity post mining (Rio Tinto 2004, 2008, 2010). In order to meet these aims, a series of avoidance zones (AZ), biodiversity offset zones (OZ) and restoration zones (RZ) have been designated. In 2015, five of the 17 forest fragments (S1, S2, S8, S9 and S17) received official protected status and are now considered IUCN Category IV protected forests (NAP Ambatoatsinanana decree no. 2015-778), requiring long term management under the direction of QMM. Previously all fragments had been governed under local community management structures. Today, both fragments S1 and S2 are heavily degraded forests and are intended to be restored under the mining scheme as RZ. Restoration work is to be conducted by local environmental consultants Tropical Biodiversity and Social Enterprise (TBSE), sub-contracted by QMM. In contrast, the fragments S8, S9 and S17 are considered to be largely intact and were selected for protection as AZ due to their structural integrity and as the best examples of the littoral forest habitat, and therefore will be circumvented by the mining project. S17, a forest fragment situated directly on the coast and featuring a narrow strip of unique strand forest - dominated by large halophytic *Pandanus* screwpines, is also in part privately owned by the de Heaulme family.

Twelve littoral forest fragments (S3, S4, S5, S6, S7, S10, S11, S12, S13, S14, S15 and S16) are situated within the proposed mining footprint, and are expected to be removed, resulting in the loss of approximately 887.5ha (57%) of standing littoral forest (this includes the loss of forest from fragments within the AZ, that will be reduced). Included are two other notable fragments, S6 and S7, which are rapidly becoming degraded as a result of being designated as community usage zone with unregulated resource extraction permitted (CZ). Under this new arrangement, the collection of endemic trees for timber and firewood is strictly prohibited within the protected forests and should instead be obtained from the CZ forests or with permission from the other unprotected fragments. Similarly, the clearing of forest for agricultural use (tavy), hunting, and the collection of specific forest materials are controlled under the local DINA as outlined in the following section. Of the total littoral forest of Sainte Luce (1552ha), some 599.35ha are set aside as AZ (38.61%) and 65.4ha (4.21%) are earmarked for restoration. In early commitments, the mining project also committed to restoring 225ha of littoral forest in Sainte Luce (Temple et al, 2012). Substantial but controversial offset zones for the wider ilmenite project are also located at two sites outside of Sainte Luce (Rio Tinto 2004, 2008), in the humid forests of Mahabo (23°11'10"S; 047°43'07"E) and Bemangidy-Ivohibe (24°34.S; 047°12.E).

Table 1.

Overview of the littoral forest fragments of Sainte Luce. GPS coordinates provide a representative geographical locality for each fragment. The table also provides an assessment of current condition. *The proportions of S8, S9 and S17, although situated within the AZ, will be reduced to 80, 225 and 295ha respectively. Size estimates derived from Google Earth Pro 7.3.2.5776.

Vernacular Forest Name	Designation	GPS Coordinates (UTM)	Size (Ha) 2000	Size (Ha) 2010	Size (Ha) 2020	Status 2015	Present Condition
Elotavy	S1	713366; 7245537	82.93	44.9	41.90	Protected RZ	Degraded
Andranopanihy	S2	713799; 7247242	36.1	28.9	23.50	Protected RZ	Heavily degraded
Ambatomena	S3	714521; 7250028	54.6	52.9	51.80	Unprotected	Degraded
Ankaifira	S4	715231; 7251887	6.89	6.32	6.20	Unprotected	Degraded
Ranomena	S5	713339; 7252274	24	22.8	22.90	Unprotected	Heavily degraded
Etazo	S6	716296; 7254100	206	165	162.00	CRZ	Partially degraded
Ambondro	S7	717243; 7256069	230	218	221.00	CRZ	Partially degraded
Agnalavinaky	S8	717513; 7258566	125.1	91.21	86.75	Protected AZ	Relatively intact but fragmented
Ambandrika (Agnalan'ambridriky)	S9	719726; 7258870	367.75	346.8	346.00	Protected AZ	Relatively intact
Amikalambo	S10	720581; 7261773	13.5	15.3	15.70	Unprotected	Degraded
Elagnora	S11	720518; 7262384	34.8	33.7	34.90	Unprotected	Degraded
Vodiala	S12	723259; 7270017	21.2	21.4	21.70	Unprotected	Degraded
Efasimalandy	S13	721307; 7265547	28.7	15.9	15.70	Unprotected	Degraded
Ankaranjato	S14	722140; 7267429	31.6	14.2	28.30	Unprotected	Heavily degreaded
Agnalamantsy	S15	722614; 7268615	83.9	61.3	68.40	Unprotected	Degraded / Fragmented
Amarofototry	S16	723259; 7270017	58.9	44.8	46.50	Unprotected	Degraded
Andranangy / Amboronteny / Agnalaro	S17	719493; 7255908	365	365	359.00	AZ / Privately owned	North intact, South degraded

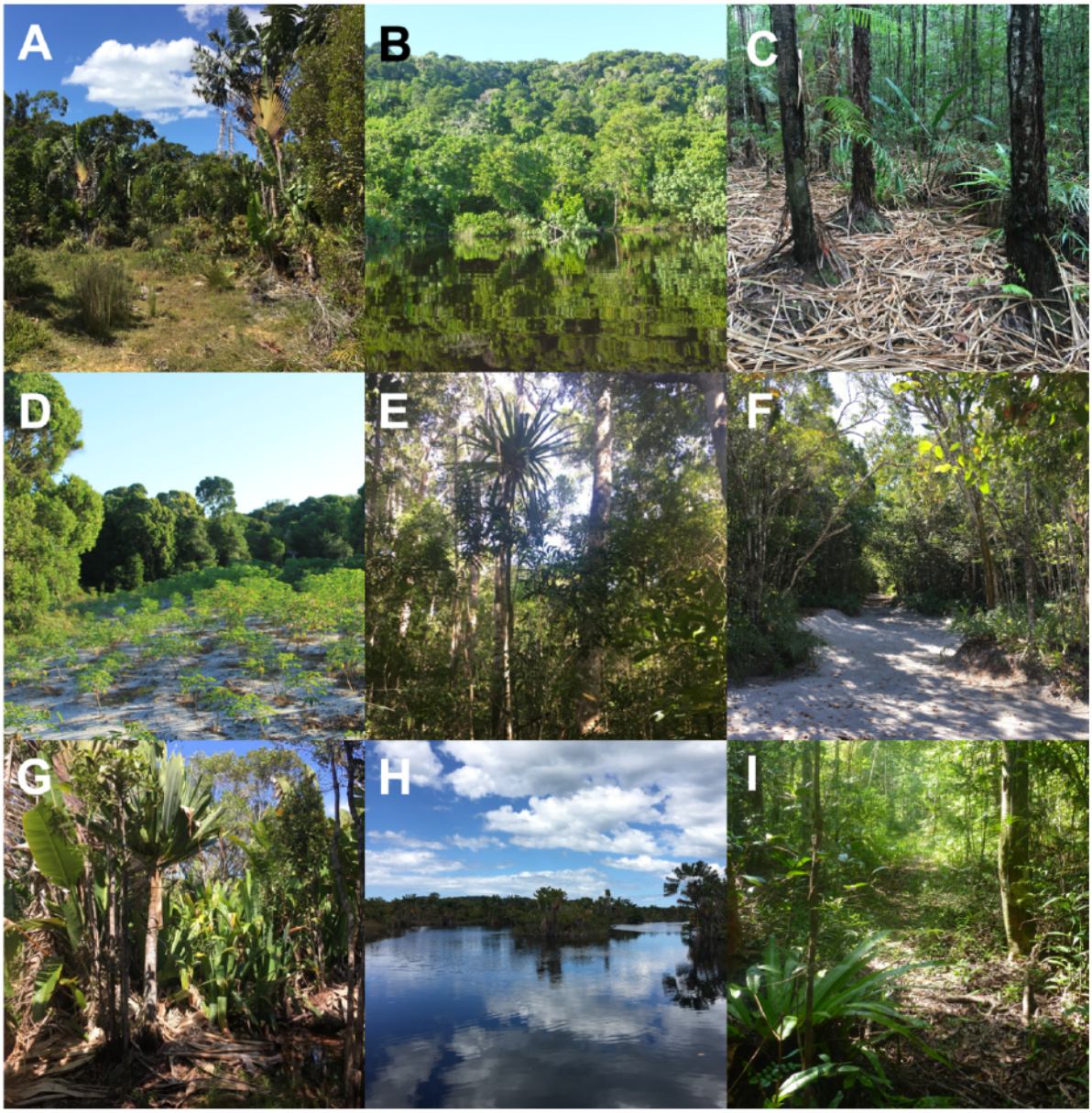

Figure 6 – The habitat of Sainte Luce: (**A**) Ravenala and open area in S7, (**B**) View of S17 forest across the estuary, (**C**) Forest interior in S9, (**D**) Open area on S8 forest edge, (**E**) *Pandanus delphinensis* in S9 interior, (**F**) Forest edge habitat in S9, (**G**) Swamp habitat S8, (**H**). Riparian habitat between S9 and S7, (**I**) Forest interior S9.

The majority of work in this study was conducted in forest fragments S9, S8, S7 and S17 respectively, largely due to the clustering of these fragments around the local community and the SEED Madagascar research station. However, many of the other Sainte Luce forest fragments were visited at least once to clarify the presence of lemurs. The Sainte Luce area is criss-crossed with rivers, swamps and waterbodies making regular surveying in some forests a logistical challenge. To reach S7 a wooden foot bridge was installed in 2015 to facilitate timber and firewood collection for the community, as the forest was allocated CZ status, however this bridge is regularly damaged and unusable, particularly following

large storms and cyclones in the wet season. Since its initial installation, the bridge has been functional for approximately 50% of the time. Similarly, in order to access S17, an estuary must be crossed by pirogue (dugout canoe).

As a result of historical and ongoing extraction practices, each of the 17 forest fragments in Sainte Luce now support differentiated communities of animals and plants. Smaller fragments are considered to support subsets of the communities present in the largest and more intact forests. However, the distribution of many animals is also determined by fragment size, structure and condition, the presence of appropriate micro-habitats, and mediated further by hunting practices. Presently four species of lemur are known to inhabit the Sainte Luce littoral forest fragments (**Fig. 7**); one species of Lemuridae, *Eulemur collaris*, two species of Cheirogaleidae, *Cheirogaleus thomasi* and *Microcebus tanosi*, and finally one species of Indriidae *Avahi meridionalis*. A second Lemuridae species, *Hapalemur meridionalis* (previously considered *H. griseus*), has previously been reported in Sainte Luce, and was last reliably observed in 2002 in fragment S8 (Ellis, 2003). However, extensive searches for the species in 1999 returned no evidence (G. Donati. pers. comm), indicating the species was likely already very rare by this time. No further observations have been since made despite a large amount of surveying effort being conducted by the NGO SEED Madagascar, TBSE and multiple independent researchers. A current assessment of lemur distribution in Sainte Luce is provided in **Table 2.**

Table 2.

A summary of lemur distribution in Sainte Luce. X = confirmed presence. Not all fragments have been assessed and further work is required to conclusively establish the presence / absence of lemurs in a number of fragments.

Forest Fragment	*Eulemur collaris*	*Avahi meridionalis*	*Cheirogaleus thomasi*	*Microcebus tanosi*
S1	X	X	X	X
S2	X	X	X	X
S3				
S4				
S5				
S6		X	X	X
S7		X	X	X
S8	X	X	X	X
S9	X	X	X	X
S10		X	X	X
S11		X	X	X
S12	X	X	X	X
S13				
S14				
S15				
S16				
S17	X	X	X	X

In addition to the work undertaken in Sainte Luce, several other interesting littoral areas and inland humid forests were visited, again in an attempt to establish the identity of the lemur's present and improve the resolution of lemur distribution in the area. These areas included Ampasy (24° 34'S; 47° 09'E), Lokaro (24° 56.310'S; 47° 6.533'E), Mandena (24° 57.455'S; 46° 59.810'E) and Nahampoana Private Reserve (24° 58.505'S; 46° 58.801'E). Included in this study and presented in **Chapter 3**, and discussed later in a number of subsequent chapters, are a series of results obtained from two short expeditions to Nahampoana Private Reserve. During these visits, ten individual mouse lemurs were captured, measured and sampled as outlined in **Chapter 2**, **Animal processing**. Initial visual inspection had indicated that these animals belonged to *Microcebus tanosi* and this has since been borne out by initial genetic (mtDNA) analysis. Nahampoana is classed as a Private Reserve and is essentially an old arboretum (approx. 50ha) established circa 1900 by French colonialist owners. The habitat here is a mixture of mature introduced species (*Albizia* sp., *Araucaria* sp., *Cinnamomum* sp., *Eucalyptus* spp. and *Psidium* sp.) interspersed with a number of transplanted species not found in the immediate area (*Adansonia* sp., *Didiereaceae* sp., *Pachypodium* sp.,) and native species, all set within an anthropogenic landscape of rice paddy fields and fruit trees. Similarly, the reserve also now supports introduced groups of *Lemur catta* and *Propithecus verreauxi*. Therefore, Nahampoana cannot be considered a natural habitat, however it is probable that the nocturnal lemur community is autochthonous. During the *Microcebus* captures, the study team observed a pair of *Avahi meridionalis,* an observation that constitutes the first known sighting of the species in the reserve. This observation is indicative of an 'open' nocturnal lemur community with links to other nearby forested sites, providing some evidence that the nocturnal species at least may occur naturally within the boundaries of the reserve.

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Figure 7 – The lemurs of Sainte Luce: (**A**) *Avahi meridionalis* (EN), (**B**) *Cheirogaleus thomasi* (CR), (**C**) *Microcebus tanosi* (EN) and (**D**) *Eulemur collaris* ♂ (EN). The identity of all lemur species is now firmly accepted, with all three nocturnal species confirmed genetically as part of this study, and the *Eulemur* species already well established (Pastorini et al, 2003).

Overview of forest management and protection in Sainte Luce

The littoral forests of Sainte Luce are subject to the same governance strategy as all other forests in Madagascar and are regulated and controlled by a hierarchical series of organised bodies (**Fig. 8**). However, the system is complex and notoriously difficult to understand with regular adaptations and changes made to each level of the structure with every political reshuffle. This overview sets out the broad shape of the governance mechanism as it has been since 2015, and in the early stages of the new

government under President Andry Rajoelina (elected December 2018). The structure is essentially controlled in a top-down manner; with ultimate decisions concerning overarching environmental issues decided by Parliament in Antananarivo, through dictates directed through the Ministry of Environment and Sustainable Development (MEDD - Ministère de l'Environnement et du Dévelopment Durable).

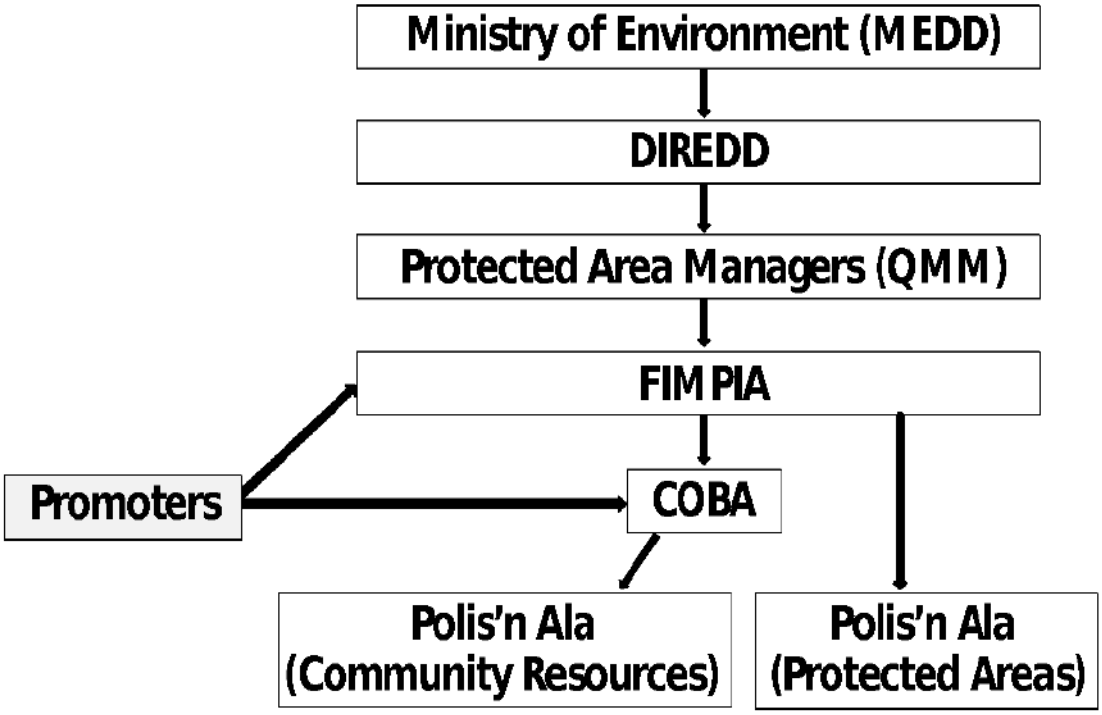

Figure 8 – The management structure and hierarchy of environmental authorities in Madagascar and within the Sainte Luce littoral forests. *Aspects of this structure are regularly adapted by incumbent political regimes.

The MEDD are the primary authorities on environmental policy in Madagascar. They are directly instructed by the government and are responsible for implementing the broad environmental strategy of the state (e.g. President Marc Ravelomanana's famous 'Durban vision' to triple Madagascar's protected area network). Furthermore, they are ultimately responsible for the management of the protected areas network and national biodiversity. The MEDD further serve to protect and maintain ecosystem services, preserve the natural and cultural heritage of sites within the protected areas, develop and enhance biodiversity by facilitating research and to contribute towards social and economic development through the sustainable use of natural resources. The Direction de l'Environnement et du Dévelopment Durable (DIREDD and formerly DREFF / DREMFF) is the body responsible for the ultimate enforcement of the directives set out by the MEDD. In the southeast, DIREDD are responsible for environmental affairs across the Androy, Anosy and Atsimo-Atsinanana regions. Its broad inter-

regional remit is to oversee the conservation of regional biodiversity. Furthermore, it aims to promote and ensure the sustainable use of natural resources and can arbitrate environmental disputes that happen at local levels.

Since a selection of forest fragments in Sainte Luce were formalised as avoidance zones, negotiated as part of the mining proposal, and subsequently recognised as IUCN Category IV Forests / Habitat or Species Management Areas, QMM have been installed as the Protected Area Managers. Habitats in this category are defined as '*protected areas aiming to protect particular species or habitats and management reflects this priority. Many category IV protected areas will need regular, active interventions to address the requirements of particular species or to maintain habitats*' (IUCN, 2019). Category IV protected forests rely on regular conservation interventions and require dedicated long-term management in order to properly protect biodiversity and ecosystem function. Management of these forests can be expensive and requires the careful monitoring of the wider ecosystem as well as specific habitats, to ensure that the proper environmental context of the area is provided. As a result, it is now the duty of QMM to prevent illegal activities within these protected sites and to implement the environmental actions and commitments outlined in their initial mining proposals (outlined in Temple et al, 2012) and biodiversity action plan (BAP).

Working below DIREDD and also under the direction from local protected area managers QMM are the body known as FIMPIA (Fikambanan'ny mpitantana Ala Ambatoantsinanana), a more localised committee that are responsible for environmental resources and the protected areas within the Ambatoatsinanana area. It is comprised of a board of advisors and an executive committee representing the eleven Fokontanys that border the Sainte Luce forests. More widely, the body governs the protected areas within the Iabokoho, Mandromadrometra and Mahatalaky districts, with Sainte Luce belonging within the later. FIMPIA also chiefly oversee the work and maintenance of the Polis'n Ala (forest police) in the protected areas and report any breaches of local law, as set out in local community Dina, to QMM and DIREDD. At the fokontany (village) level, forest governance is mediated by COBA (Communauté de base). In Sainte Luce the COBA, similar to FIMPIA, is comprised of representatives from local fokontany's. Most representatives are community leaders (village chiefs) or village elders. The COBA holds regular meetings and ultimately determines the distribution of local resources and are responsible for the maintenance of Polis'n Ala patrols within the non-protected habitats. COBA are responsible for overseeing the environmental concerns of the Sainte Luce commune and the sustainable governance of natural resources. COBA are also responsible for upholding local environmental laws (codified in the *Dina*). In Sainte Luce the most pertinent environmental actions that are strictly prohibited include unlicensed resource extraction (the harvesting of certain valuable tree or plant species), hunting, unchecked zebu grazing, uncontrolled fires, charcoal manufacture and the

inappropriate disposal of rubbish and waste (**Fig. 9**). In most cases disputes are settled locally but may be elevated to FIMPIA or QMM if they cannot be resolved.

At the base level, the forests of Sainte Luce are patrolled by small groups of Polisin'ala (forest police), organised and compensated by either FIMPIA or COBA depending on the forests that they patrol. Sainte Luce is now complicated by the fact that it now has a two-tier patrol system, with both protected and unprotected forests with differing regulations and patrol practices. Patrols conducted within the protected forest fragments are the responsibility of FIMPIA, whilst those in the unprotected and community forests are the responsibility of COBA. At present, over 60 Polisin'ala agents are employed within the Ambatoatsinanana area (T. Endor. pers. comm). The main objectives of the patrol groups are to deter and intercept any individuals engaged in banned activities. However, in reality the system has a serious flaw. Despite the majority of the Polisin'ala agents being well trained, possessing excellent local knowledge and being committed to their roles, the fact that they patrol within the close-knit communities where they live means that they are often unlikely to report individuals that they know personally, are related too or that hold a respected positions within the community. Given the level of poverty within the Sainte Luce community, the economic and social repercussions of reporting a known person for a minor discretion may seem draconian, and ultimately undermines the protections in place.

Figure 9 – Signs displaying local prohibitions in both visual and written form on the edge of protected forest S9 in Sainte Luce. Any infraction is liable to be punishable by the local COBA with sanctions set out in the local Dina. The images depict (left) illegal logging, hunting, and zebu grazing and (right) no cutting of trees, no removing tree bark, no landfill and no charcoal production.

Given that the community of Sainte Luce relies so heavily on the forests for natural resources, and with demand increasing with the population, the robustness of the hierarchy structure and its ability to identify threats and to protect the environment and natural resources is extremely important, particularly at local levels. The potential for illegal logging and hunting is also anticipated to increase as the supply of forest resources becomes diminished. This is a widely acknowledged point amongst local stakeholders, and it is the objective of many to support and strengthen these bodies and to enable them to develop their roles. With the proposed mine set to remove a substantial proportion of current littoral forest cover, and with the majority of offset zones outside of the Ambatoatsinanana area, the capacity of local associations to protect their resources and interests is more crucial than ever before.

Focal study species - *Microcebus tanosi*

Microcebus tanosi or the Anosy mouse lemur is a recently identified species (Rasoloarison et al, 2013), whose initial description originates from the lowland rainforests of Manantantely (type locality - 24°98′S, 46°92′E) and Ivorona (24°83′S, 46°95′E). The type specimen (*Holotype* RMR 209 – an adult female) is held at the Department de Biologie Animale at the Université d' Antananarivo. At present, almost no ecological knowledge exists within the published literature for this species. A relatively large mouse lemur, with a distinctly rufus coloured pelage, *M. tanosi* has previously been overlooked by researchers who have often attributed the species to the outwardly similar *Microcebus rufus*, a species whose range was until recently considered much larger and is now known to occupy forests further north. Previous works conducted on the species now recognised as *M. tanosi*, refer to the species in the literature as either *M. rufus* (Lewis Environmental Consultants, 1992b; Andrianasolo et al, 2006; Hapke et al, 2011; Rakotondranary et al, 2011), *Microcebus* cf. *rufus* (Hapke et al, 2012; Sommer et al, 2014) or *Microcebus* sp. (Ganzhorn et al, 2007; Nguyen et al, 2013). A new illustration of *M. tanosi*, depicting general morphological and phenotypic features is presented in **Figure 10**, whilst **Figure 11** provides some photographic examples of the species in the wild.

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Figure 10 – *Microcebus tanosi*. Illustration by Stephen D. Nash.

- Linnaean classification.

Kingdom: Animalia

Phylum: Chordata

Class: Mammalia

Order: Primates

Suborder: Strepsirrhini

Family: Cheirogaleidae

Genus: *Microcebus* É. Geoffroy, 1834

Species: *tanosi* Rasoloarison, 2013

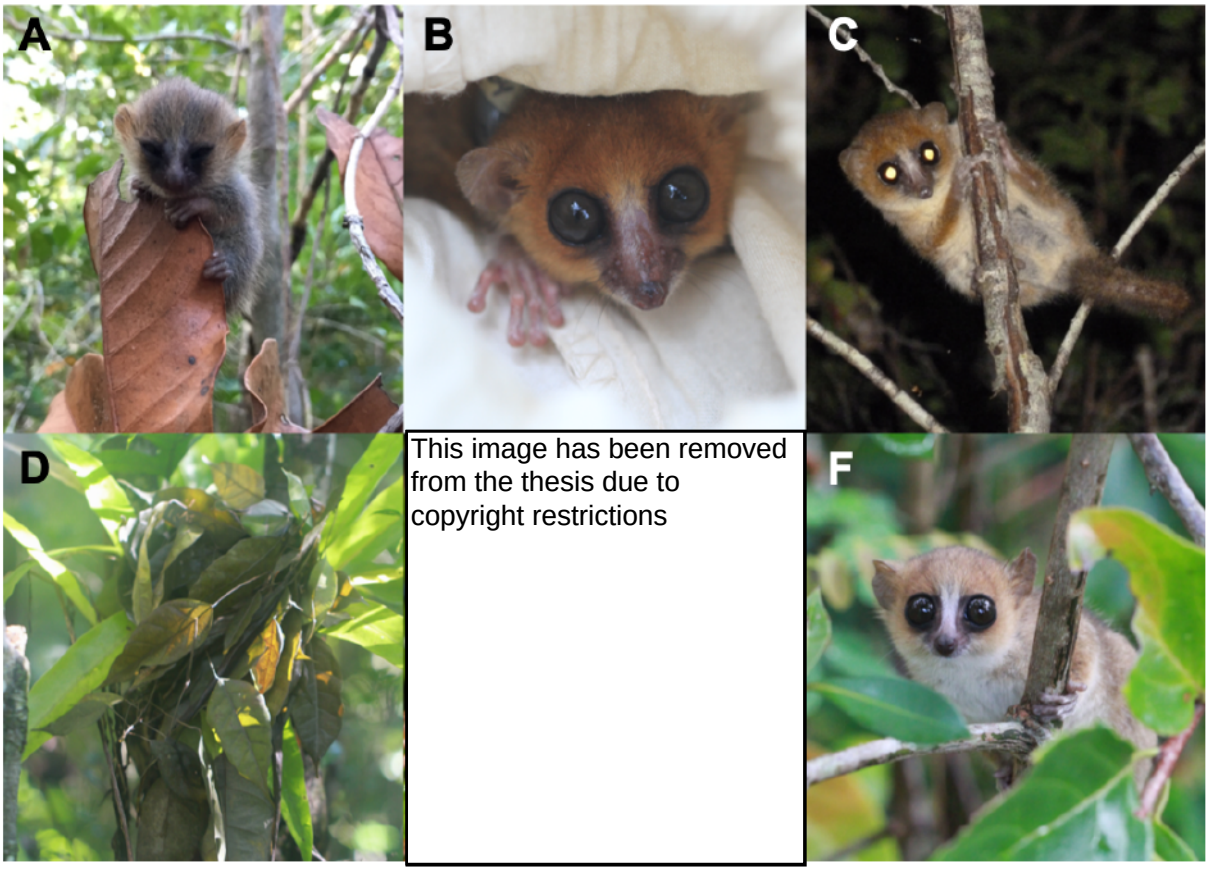

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Figure 11 – *Microcebus tanosi*. **A**) Infant in Sainte Luce, Nov 2018. **B**) Adult on release after being fitted with radio-collar, Sainte Luce, Oct 2016. **C**) Adult observed foraging in Sainte Luce, Sep 2015. **D**) Example of leaf nest, Sainte Luce, Aug 2018. **E**) Individual photographed in Ampasy, Apr 2019. **F**) Individual from Nahampoana Private Reserve, Aug 2019. All photographs by SHR except; **E** by Claire Cardinal.

Although very little was known about this species, it was assumed that it would largely conform to the general pattern of behaviours and share the same distinctive characteristics as other mouse lemur species

across Madagascar. All mouse lemurs, like most nocturnal strepsirrhines, are diminutive in size, strictly nocturnal, omnivorous and exist within discreet social networks. Divergence from any of these characteristics would constitute a real surprise. Notwithstanding activity pattern, each of these traits does however vary to some extent between species, and understanding the range and plasticity of biometric traits, ecological character and social behaviours provides a fuller understanding of the genus as a whole. This in turn enables a more complete understanding of the evolutionary processes which have shaped mouse lemur evolution across Madagascar. An up-to-date phylogeny of *Microcebus* is presented in **Figure 12** (unpub. Jelmer Poelstra, January 2020).

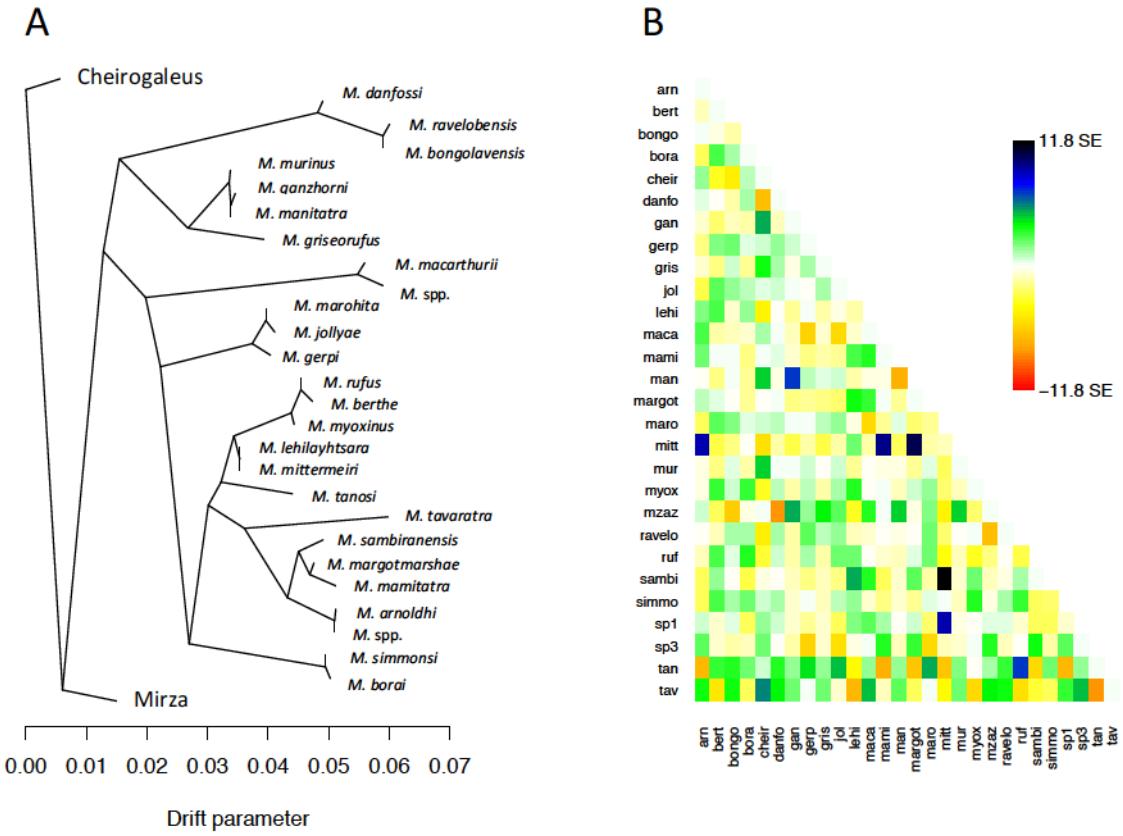

Figure 12 – Most up-to-date understanding of *Microcebus* phylogenetic relationships with *Cheirogaleus* and *Mirza* as outgroups. Figure produced by J. Poelstra and unpublished. **A**) Treemix figure depicting the systematic relationships of recognised mouse lemur species. Drift parameter represents weighted estimates of admixture events. **B**) Residual covariance between each lineage pairs. Positive values suggest closer relationships than suggested by the tree, i.e., admixture. Data indicates some genetic interaction between *M. tanosi* and *M. rufus*.

Species distribution and conservation status

The recent identification of *M. tanosi*, along with several other novel forms within a very limited geographical area (Hotaling et al, 2017) illustrates the complex biogeographical situation that exists in southeastern Madagascar. The distributional boundaries of *M. tanosi* are not fully resolved, particularly in the north, but are broadly determined in the south. This study has confidently ascertained that *M. tanosi* solely occupies the littoral forests of Sainte Luce, whereas previously the prospect of sympatric species remained a possibility. To the south of Sainte Luce, the species distributional boundary extends down the coastline as far as the Lokaro estuarine system (24° 54.515'S; 47° 7.028'E). Whilst it appears that the Lake Mananivo estuary and river system in Lokaro presents a definitive physical boundary between *M. tanosi* to the north (in Sainte Luce) and *M. ganzhorni* (proposed by Hapke et al, 2008 and confirmed by SHR in 2017) to the south, the situation inland is less well defined and the distributional relationship between neighbouring species requires further clarification. Inland, it appears that the southernmost distribution occurs in the relict rainforests of Manantantely, a now isolated parcel of forest detached from the extreme south of the Vohimena mountain range (**Fig. 13**).

Although there are many large river systems in the region, originating from the high Vohimena mountains, it appears the species boundaries inland are largely defined by habitat type (Rakotondranary, et al, 2011) and it is clear that there are multiple contact zones between species. Ten mouse lemur individuals captured and sampled in Nahampoana as part of this study revealed, somewhat surprisingly, that the species occupying this non-natural parcel of forest, all belong to *M. tanosi*. Nahampoana is situated less than 2km west of the remaining littoral forest parcels of Mandena, the type locality for *M. ganzhorni* (Hotaling et al, 2017), and it is almost inconceivable that some migration does not occur between these forests. Details pertaining to this sub-population of *M. tanosi* are further detailed in **Chapter 3**. Notably, the individuals show distinct phenotypic differences from both the sampled individuals from Sainte Luce and the holotype described from Manantantely (Rasoloarison et al, 2013).

It is highly likely that *M. tanosi* occupies the entire forested Vohimena mountain range (encompassing the Tsitongambarika Protected Area) and Anosyenne range (including the rainforest parcel of Andohahela National Park), and all of the littoral forests of Sainte Luce as well as the isolated remnant forests of Manantantely and Nahampoana. A recent assessment of a relatively small (~1080Ha) and isolated patch of rainforest (22° 36.665'S; 46° 43.581'E) some 260km north of Manantantely, and 20km to the west of the main eastern mountain chain, provides the most northerly confirmation of the species to date (P. Wright. pers. comm). Combined these areas cover some 680,000Ha, however the northern portions of this distribution require further study, and its relationship with *M. rufus* needs further investigation, as the distributions of both species seemingly overlap (Kamilar and Muldoon, 2010; Louis and Lei, 2016). It is also unclear to what extent population density may vary across the species'

range, and to what effect if any, habitat type has on such demographic variables. However, an examination of the species broad distribution indicates that *M. tanosi* is largely a rainforest or humid forest species with the vast majority of its known habitat being classified as such, with only the highly fragmented and limited littoral forest fragments of Sainte Luce, and the artificial botanical gardens at Nahampoana providing alternative habitat types.

The formal conservation status (IUCN categorisation) of the species had not been determined at the outset of this study, however after appraisal at the Red List workshop held in Antananarivo in May 2018, the species has been listed as Endangered (EN B1ab (i,iv)) (Donati et al, 2020c). All known sampling sites are depicted in **Figure 13**. The sites at Manantantely (24° 59.056'S; 46° 55.448'E) and Ivorona (24° 50.090'S; 46° 57.451'E) provided the initial samples (n=6 at Manantantely and n=4 at Ivorona) for the species description (Rasoloarison et al, 2013). Early samples collected by Rakotondranary et al (2011) in Mahamavo (24° 44.179'S; 46° 43.331'E) and at Ivolo and Enato by A. Hapke and N. Andrianjaka in 2009 were all originally identified as *M. rufus* but should now be considered *M. tanosi*. Further samples were obtained from a small number of individuals (2-3) and verified by a research team led by Dr Ed Louis circa 2015 (24° 35.596'S; 47° 8.881'E) at Ampasy, in the northeast of the Vohimena mountains (Tsitongambarika Protected Area). The mouse lemur research group 'RADSeq Consortium' led by Dr Jordi Salmona also possess a collection of samples from Andohahela NP (24° 46.201'S; 46° 51.805'E) but specific details relating to the collection are unknown. This study adds new distributional confirmation for the presence of *M. tanosi* in the littoral forests of Sainte Luce and the arboretum at Nahampoana Reserve. Finally, recent confirmation of *M. tanosi* by a team of researchers from Centre ValBio and Stoney Brook University, in the 'Lost Rainforest' near Ivohibory represents the most northerly known locality of the species (**Fig. 13**).

Microcebus tanosi shares the same geographical area (<20km^2) with at least another four distinct mouse lemur species, yet no evidence so far exists for gene flow between *M. tanosi* and the other proximal species besides the phenotypic observations recently identified at Nahampoana. Analysis undertaken during the initial description of *M. tanosi*, using samples from Manantantely and Ivorona found no evidence of introgression (Rasoloarison et al, 2013). This complex spatial pattern of mouse lemur species in the southeast suggests that current distributions are likely a consequence of the region's dynamic environmental history (Virah-Sawmy, 2009), with the migration and invasion of species into a shifting and dynamic array of habitat types as forests expanded and contracted over the past 5,000 years (Hapke et al, 2012).

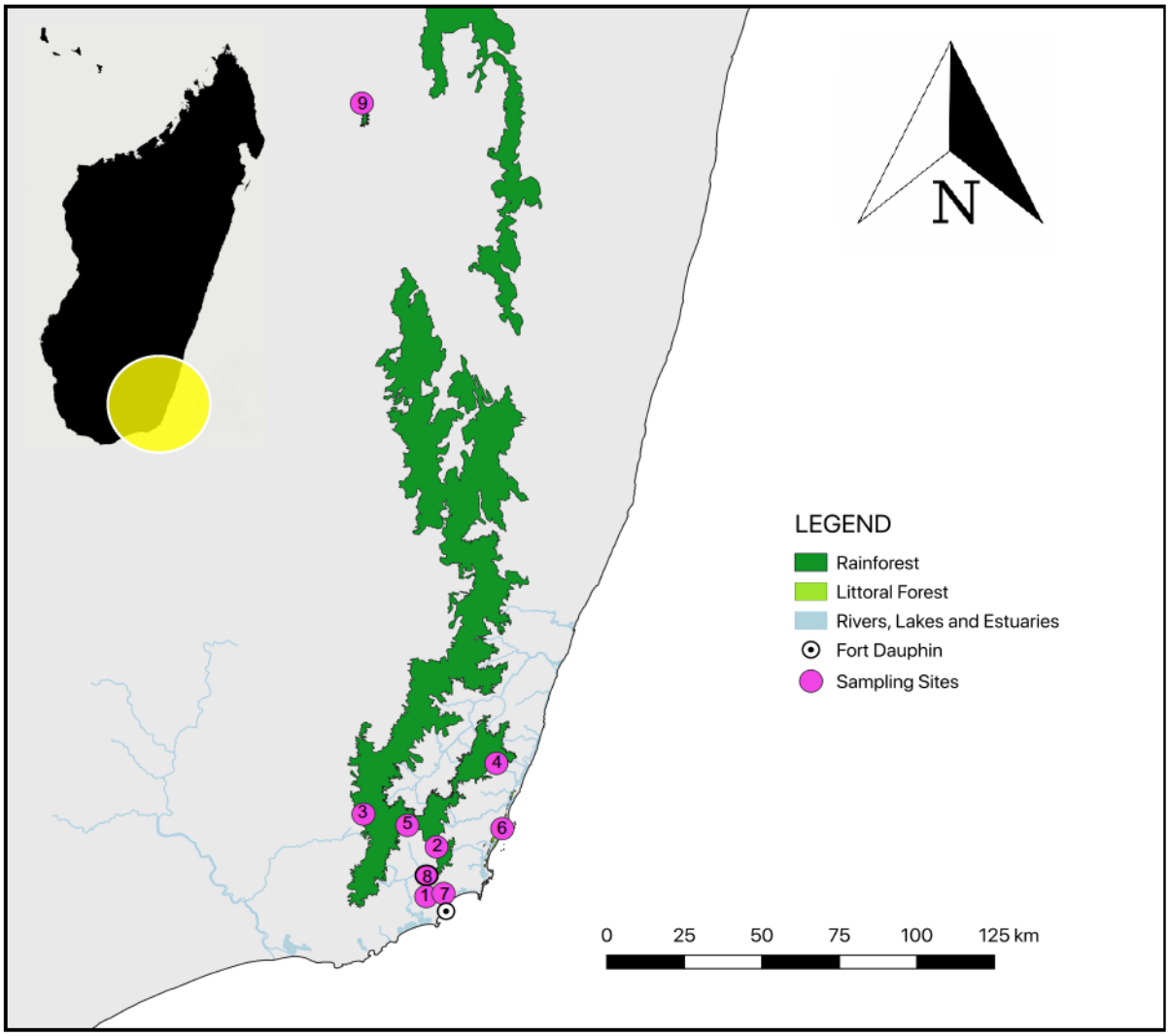

Figure 13 – The known distribution of *Microcebus tanosi* including the northern locality near Ivohibory. Sampling Sites: **1**) Manantantely, **2**) Ivohibe, **3**) Mahamavo, **4**) Ampasy, **5**) Andohahela unspecified site, **6**) Sainte Luce, **7**) Nahampoana Private Reserve, **8**) Ivolo, and **9**) the 'Lost Rainforest' near Ivohibory. The Enato site is not represented.

Trapping and capture methodology

The focal species (*Microcebus tanosi*) was targeted using a core standardised trapping methodology, employing large sized, folding galvanised Sherman Traps (7.6cm x 8.9cm x 22.9cm). Sherman trapping is a commonly adopted technique to capture small mammal species (Sutherland, 2006; Martin et al, 2011; Larsen, 2016) and has been used widely across Madagascar to capture *Microcebus* spp. (Eberle and Kappeler, 2004; Lahann et al, 2006; Gligor et al, 2009; Rakotondranary and Ganzhorn, 2010; Blanco, 2011; Ganzhorn et al; 2012; Burke and Lehman, 2014; Radespiel et al, 2018). Given their

trophic position as consumers, with a general preference for a fruit-dominated omnivorous diet (Mittermeier, 2010) and the ubiquitous nature of the method, Sherman traps were an obvious choice for the live captures in Sainte Luce. The principal aim of trapping was to capture mouse lemurs, and to collect genetic and biometric material, firstly to confirm species identity (see **Chapter 1**, **Project genesis**) and secondly to enable a first in-depth ecological study of the species in Sainte Luce. A selection of suitable captured individuals would be fitted with Ultra High Frequency (UHF) radio collars and subsequently act as study animals on their release.

Traps were consistently deployed in pairs and in sets of 20 per location, with each trap pair set at 10m intervals. A total of 42 trapping locations were surveyed across the three forest fragments, S7, S8 and S9 (**Chapter 3**), resulting in a total 3,360 trap nights (no. traps x no. nights). All traps were deployed in natural forest and set amongst varied forest architecture (low and high branches, against tree trunks, on dead trees, lianas and vines and in leaf axils e.g. *Pandanus* spp.) ranging from between 0m to 4m above ground. Traps were opened (set) and baited with banana in the early evening and then checked for animals early each morning for a period of four consecutive nights. Trapping can affect community species composition if conducted for extended periods and resulting captures can include individuals not originally associated with the locality. During the birthing season (Dec-Apr), traps were checked very early to limit the amount of time adults and weaning infants may be separated. Additionally, trap dyad locations were assessed after 24 hours, and modified if local factors posed a potential problem to the well-being of captured animals (e.g. ants swarming over trap bait, or if the site seemed prone to heat exposure). All traps were cleaned using chlorinated water, and thoroughly rinsed between deployments. In rare cases Sherman Traps have been known to inflict wounds and injuries of captured animals, particularly the endemic Tuft-tailed rats (*Eliurus* spp.) (J.B. Ramanamanjato. pers. comm) so in order to minimise this risk, a layer of clear Sellotape was placed over the sharp edges around the door frames but did not interfere in trap functionality. A total of 42 trap sites were selected based on expert advice in an attempt to target mouse lemurs. All forested habitat was assumed to be suitable for *M. tanosi*, however forest quality varied amongst trap locations. Trapping was carried out in 2015 (April-October), 2016 (September-November), 2017 (August), 2018 (August-October) and 2019 (May) by SHR. The GPS location of each individual trap was recorded using a Garmin GPSmap 62s.

As of 2016, a complementary method for capturing mouse lemurs was trialled and adopted. A direct capture approach enabled a more active solution to increasing the number of captured individuals and was conducted in parallel with the set Sherman Traps. Direct captures were attempted in areas where mouse lemurs were regularly observed during specific lemur transects and night walks (**Chapter 6**). A small catch team of three to four people, led by SHR and Retsiraiky Jean Rossizela would set out just prior to dusk, and begin slowly patrolling forest trails in areas of disturbed forest, close to the forest

edge. In these areas, canopy height is generally lower, and trees are more sparsely distributed, meaning that mouse lemurs using these trees are less difficult to apprehend as forest complexity is reduced. The group used torches to increase the chance of observing a mouse lemur at distance, utilising the anatomy of the mouse lemur, and the retroreflective retinal layer, the *tapetum lucidum,* to increase detection success. Once an individual was identified, a team member would hold the attention of the lemur with torchlight, while the other groups members would carefully position themselves to cut off escape routes to trees and nearby areas of high foliage density. With a steady but deliberate approach, it is possible to capture the lemur by hand. Gloves were a pre-requisite for this methodology as hand captured animals frequently bite. This technique is uncommon but does have precedence in Madagascar (Louis et al, 2006; Louis et al, 2008; R. Rakotondravony. pers. comm). Direct capture circuits were limited to 90 minutes and only carried out a maximum of three times each week to limit the impact of disturbance on the local lemur community.

Animal processing (biometric assessment and biopsy procurement)

After every successful capture, animals were carefully transported to the SEED Madagascar research station on the outskirts of Ambandrika village, in the southern section of forest fragment S9 (**Fig. 5**). Animals were transferred using breathable cloth bags. If an animal was captured by means of trapping, the entire trap was carried back to the research station, where the animal could be extracted safely and with less risk of escape. Processing protocol included formal species identification (based on morphological assessment), the collection of genetic material (hair and tissue) and the recording of a full suite of biometric data (described and presented in **Chapter 3**). In the event of capturing a mouse lemur or another lemur species, a full suite of biometric measurements was recorded. A total of 38 biometric characters were recorded for each male individual, and 35 for females (as a result of sexual characteristics) following and adding to the range of measurements described in Burkovicth, 1989; Rasoloarison et al, 2000; Wrogemann et al, 2001; Hapke et al, 2005; Gligor et al, 2009. Morphometric measurements included important class data pertaining to sex, maturity and reproductive status, important for later comparative analysis. In the event of capturing a rodent species (endemic or invasive), a reduced number of biometric measurements were recorded (14) and a number of individuals per species were sampled (n=5) for genetic material (hair and tissue) to confirm species identity.

During the processing procedure, handling time was kept to a minimum whilst noise and disturbance was limited as far as possible in order to minimise animal stress factors. All captive animals were offered rainwater using a 10cl syringe and provided with calories (banana). Biometric measurements were obtained using a combination of digital Vernier callipers, a clear 30cm length ruler and a variety

of spring balance Pesola (20g, 50g, 100g, 200g and 500g). All measurements were recorded by a team of at least two to three research staff and data was immediately digitised. All animals were handled with great care and all appropriate precautions were taken, both for the animal, and the handler with welfare the top priority throughout. Rugged gloves were worn at all times to prevent injury from biting and scratching and to reduce the risk of zoonosis and transmission of infection from the body fluids and excreta of small mammals (Mills et al, 1995). Alcohol hand sanitizer was used regularly throughout the process to maintain personal protectiveness. Under the direction of the permit authorities, and the 'Direction Régionale de l'Environnement et des Forêt' (DREF) Tôlanaro, Anosy, it was advised that all captured invasive animals be destroyed. Given the lack of resources and facilities at the research camp, cervical dislocation was deemed the most humane and ethical way to carry out this directive, meeting the criteria set by the United States Department of Agriculture (U.S.D.A.). Invasive species were destroyed prior to processing.

Genetic materials were collected using a standard sampling protocol; hair samples were extracted from the ventral abdominal area using flat tipped stainless-steel tweezers (pre sterilized). Approximately 20 hairs were obtained for each sampled individual. Great care was taken not to accidentally pinch the cutaneous layer during extraction. Hair samples obtained for mitochondrial DNA (mtDNA) analysis were dry stored (no solution) in appropriately labelled 1.5ml Eppendorf Tubes®. Tissue samples, for nuclear DNA (nDNA) analysis were collected in the form of ear biopsies (described in.litt by Christian Roos 17-04-2016). A 5% lidocaine solution (Supernumb®) was applied to both sides of a single ear using a cotton bud during the biometric data collection phase. A minimum of five minutes were left to elapse before a thin lateral section of the helix was removed using surgical scissors. The small amount of tissue was then directly transferred to a 1.5ml Eppendorf Tube® containing 95% medical grade alcohol (EtOH). In some instances, the sample was cut into two pieces with the second samples stored in *RNA*later® RNA Stabilization Solution. Post-operative relief was applied to the animal in the form of Bactine® solution (an analgesic and antibacterial spray), again applied using a cotton bud. Fecal samples were collected opportunistically if the opportunity arose during the processing window. Fecal samples were dry stored, again in 1.5ml Eppendorf Tubes®. Equipment was sterilized using 95% alcohol between all procedures. All samples were refrigerated within a week of initial collection.

All endemic animals were returned to within 10m of their initial capture sites post-processing. Releases were conducted at an appropriate time of day to reduce predation risk, determined by the species normal activity schedule, and always within twelve hours of capture. This time frame also enabled a period of post-operative monitoring, and an opportunity to offer further water and some additional sustenance before release.

Radio-collaring.

The collaring procedure was based on and adapted from the guidance provided by HOLOHIL and on the species-specific information provided at the time of the purchase of the radio-collars. HOLOHIL PD-2C transmitters were selected due to their suitability for the focal species. The units were ultimately chosen based on the critical compromise between weight and battery lifespan and given the success of the transmitters in other published studies focusing on other small mammal species, birds, herptiles and fish (Witmer and Pipas, 1999; Rhodes, 2007; Adelman et al, 2008; Rachlow et al, 2014; O'Mara et al, 2014; Hammond et al, 2016; DeVries and Bartelt, 2018). The units weigh approximately 3.2g and had a battery life of between 4-6months, extended to 6months with modifications to the transmitted pulse frequency. The dimensions of the transmitters were 23mm x 12mm x 6mm (LxWxH). Transmitter frequencies ranged between 149.679 to 150.960MHz with a pulse frequency of 0.4per second. HOLOHIL transmitters are encapsulated in an inert waterproof epoxy (**Fig. 14B**) and were attached as neck collars using PVC (polyvinyl chloride) tubing and fine metal wires (**Fig. 14A+F**), raising overall collar weight by between 0.05 to 0.1g. The PVC tubing was selected for comfort as it has a degree of malleability whilst the internal wires prevent removal by chewing.

All animals were fully conscious throughout the collaring process. Collaring requires a two-to-three-person team and was always carried out in the secure SEED Madagascar research station. All collaring was done by SHR with assistance by H. B Longosoa and R. J. Rossizela. On each occasion the process took place after the animal had received a full biometric assessment and crucially after the animal had been carefully weighed to ensure it was a suitable candidate for collaring. For an animal to wear a radio-collar it had to weigh over 64g, ensuring that the radio collar weighed less than 5% of the animal's body mass. Only individuals over the threshold weight were selected to carry the radio-collars in line with recommended guidelines (Kenwood, 1987; Wilson et al, 1996; Sikes, 2016; Animal Ethics Infolink). This also had the advantage that the study animals could be considered as fully adult, and so collars could be attached without the necessity of allowing for ample space for growth, and with it the increased likelihood of escape from the collar. The neck circumference of the animal was also measured during the biometric assessment, using a thin wire to accurately determine the size of the necessary collar. The dense fur of the animal can make it easy to overestimate the neck circumference meaning that the resulting collar is not tight enough. All collars were custom fit to the individual mouse lemur to wear. All equipment was fully prepared and tested prior to fitting and the collar was prepared whilst the animal was safely isolated in a breathable cloth bag to minimise stress.

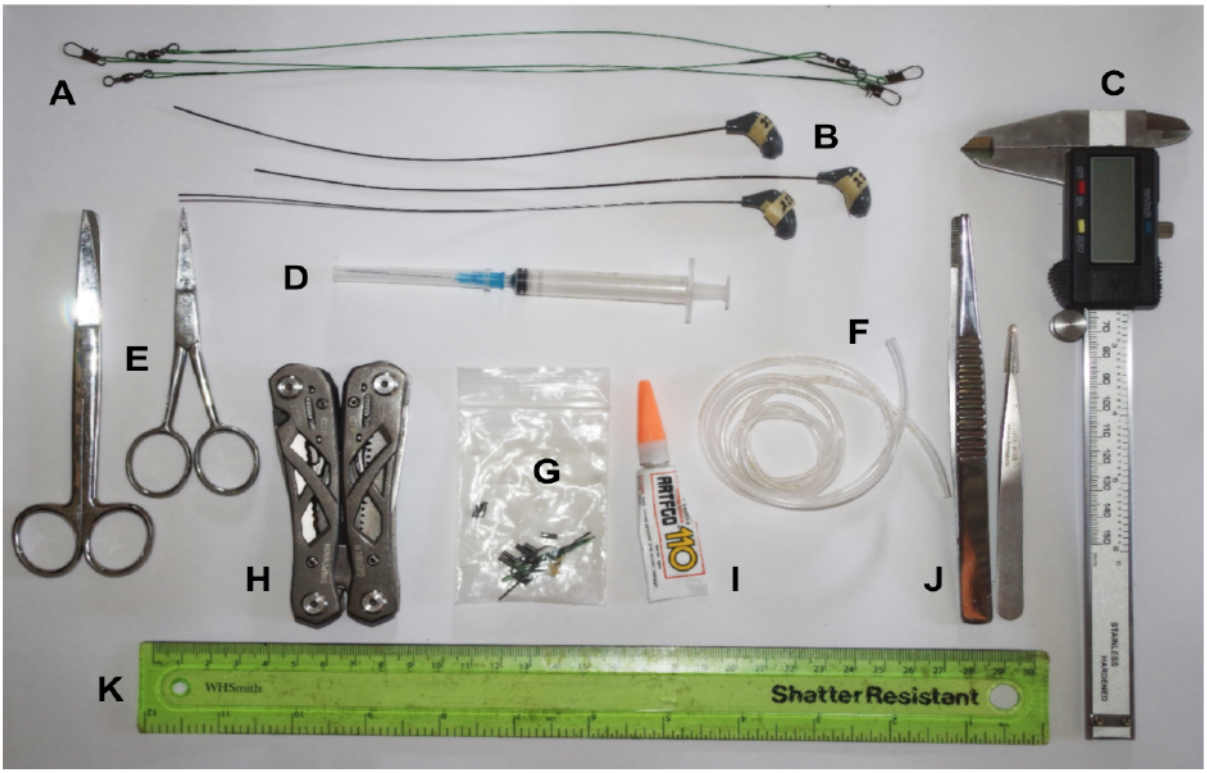

Figure 14 – Essential collaring equipment. **A**) Heavy duty fishing wire. **B**) HOLOhill PD-2C VHF radio-collars. **C**) Digital callipers. **D**) Syringe. **E**) Dissection scissors. **F**) PVC tubing. **G**) Crimps. **H**) Multitool with pliers. **I**) Superglue. **J**) Tweezers. **K**) Ruler.

First, a length of PVC tube was cut to match the neck circumference of the individual mouse lemur, minus the length of the transmitter. A syringe was used to make a hole in the PVC tube for the antenna to protrude and for the metal wires to enter and exit. A length of lightweight metal wire (heavy-duty fishing wire was used to prevent the removal of the collar by chewing) was next looped through both the tubing and transmitter, enabling the collar to be tightened and loosened once fitted. A small metal crimp that fitted precisely into the PVC tubing was threaded onto the wire and into the PVC tubing. The resulting collar was then fitted onto the animal. A single person wearing gloves was responsible for holding the animal firmly but in a secure and safe position during the procedure. Small adjustments could be made to the collar circumference by reducing the length of the PVC tube using scissors, once removed from the animal and before final collar closure. Once satisfied with the fitting of the collar, a set of pliers were used to carefully compress the metal crimp inside the PVC tubing (being careful not to hurt the animal) and to fix the collar in place. The crimp serves to clamp and fasten the metal wire within collar so that the circumference is set. The additional wires were then cut flush to the tubing so as not to protrude.

To further secure the collar, a small amount of super glue was applied to the attachment points of the tubing to the transmitter, and at the entry points where the wire was cut (again being careful not to any glue on to the hair of the animal). Examples of fitted radio-collars on study mouse lemurs are presented in **Figure 15**. The position of the collar was designed so that it could move freely around the neck but was tight enough to prevent being removed over the head of the animal. This also enabled the mouse lemur to wear the collar in the most comfortable way possible.

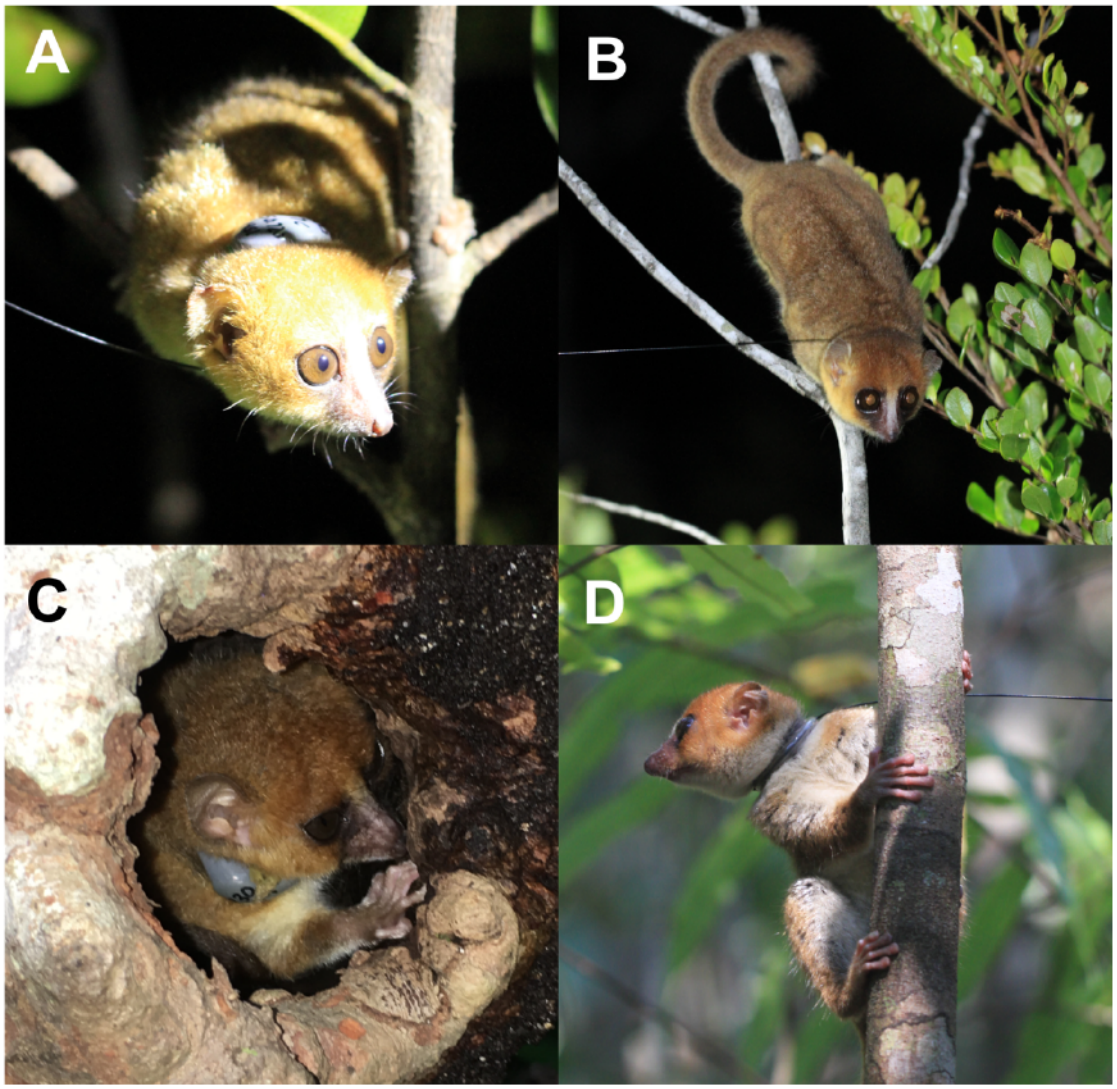

Figure 15 – Examples of mouse lemurs wearing their HOLOHIL PD-2C radio collars in the littoral forests of Sainte Luce during this study. **A**) An adult female wearing her collar dorsally. **B**) An adult male with the transmitter in a ventral position. **C**) An adult male at its sleeping site, with the transmitter in a sideward position. **D**). An adult female showing the PVC tubing around the neck, with the transmitter positioned dorsally.

Mouse lemur predators in Sainte Luce

An array of species exists in Sainte Luce that could potentially predate *Microcebus tanosi* (**Table 3**). Here I examine the community of potential predators in order to qualify the impact that these may have on the broader behavioural ecology of *M. tanosi*, providing a foundation for the ecological hypotheses generated in subsequent chapters. The assessment is based on over six years working in Sainte Luce and a variety of data sources, including literature sources, longitudinal avian and herpetological data, evidence from camera traps, observations, and findings from community initiatives such as educational sessions. Anomalous predatory observations pertaining to mouse lemurs from the literature, such as the case of observed cannibalism (Haemaelaeinen, 2012) and the reported incident of potential predation by spider (Pisauridae or Theridiidae spp.) on *M. lehilahytsara* (Crane and Goodman, 2013) are not treated, as I do not consider these consistent or major predatory threats. Similarly, *Canis lupus familiaris* is omitted from the list despite a report of a village dog taking a mouse lemur at dusk in secondary forest (Goodman et al, 1993), as it is more likely to have been an act of rare opportunism rather than hunting.

Of the 15 recognised birds of prey, only the three owl species are strictly nocturnal, and must therefore regularly encounter mouse lemurs. All three species are considered generalist feeders and are known to predate invertebrates and small vertebrates including mammals. Of these, only *Asio madagascariensis* has been documented as specifically predating mouse lemurs in the southeast of Madagascar (Goodman et al, 1991), however it is highly likely that both other species regularly predate mouse lemurs. Of the seven Accipitridae species, all must be considered at least opportunistic predators of mouse lemurs, despite no precise records being available for most species. Of the three true Accipter species (*A. francesiae, A. henstii and A. madagascariensis*) only *A. henstii* can be considered a truly significant lemur predator (Morris and Hawkins, 1998) and known to consume mouse lemurs as part of its generalised diet (Rand, 1936). Although uncommon in Sainte Luce, the species is an extremely agile and adept forest specialist and must be considered an important predator of *M. tanosi*. In contrast, there are no known records of predation on mouse lemurs by either *A. francesii* or *A. madagascariensis* although both may predate *M. tanosi* opportunistically. During this study, a signal from a radio-collared mouse lemur was detected coming from a shallow swamp directly beneath a confirmed sparrowhawk nest, providing indirect evidence of mouse lemur predation. Due to the depth and limited visibility in the swamp, the collar and remains of the lemur could not be recovered, however adult sparrowhawks were regularly seen bringing prey items to the nest above the signal origin.

Both *Buteo madagascariensis* and *Polybroides radiatus*, much larger species with diurnal activity patterns, are also both known to take small lemurs. *Polyboroides radiatus* in particular is known to consume a huge variety of species, including mouse lemurs (Karpanty and Goodman, 1999). Despite its large size this species actively seeks prey beneath the canopy, climbing around the trunks of large

trees, investigating tree holes looking for prey. Similarly, several diurnal lemur species are known to respond vocally to the presence of *B. madagascariensis*, indicating a perceived predatory threat. Given its large dietary range, it would not be surprising if this species also consumes mouse lemurs opportunistically. In contrast, the other large diurnal Accipitridae species, *Milvus aegypticus parasitus* is unlikely to be a significant mouse lemur predator, more often associated with carrion, invertebrates and livestock (Goodman et al, 1997). Of the four falcon species, *Falcon newtoni* is the only species likely to threaten *M. tanosi* in Sainte Luce. Known to hunt actively around dawn and dusk, it is commonly observed in Ambandrika village and near to the forest edge where *M. tanosi* is also regularly seen, although it appears to specialise in insects and small vertebrate prey (Goodman et al, 1997; René de Roland et al, 2005). In contrast, the other falcon species are generally considered aerial predators, capturing small birds and insects on the wing (Rand, 1936; Benson et al, 1976; Goodman et al, 1997). Finally, *Vanga curvirostris* is a known predator of small vertebrates, and a reliable observation made by L. Durrell (Goodman, 1993) describes the nest predation of *M. tanosi* at the type locality of the species, Mananatantely. Although this bird is seldom seen in Sainte Luce, it is regularly heard, and should be considered a bone-fide diurnal mouse lemur predator.

In contrast, the two species of snake have both been directly observed predating mouse lemurs in Sainte Luce (S. Hyde Roberts. pers. obs) and must be considered highly important predators. *Ithycyphus oursi* is considered a dangerous snake by local people, and its venom is likely effective against smaller, fast moving and agile prey species (Domergue, 1973; Mori and Mazuta, 2006). Whilst it is an active diurnal predator, *Sanzinia madagascariensis* is a nocturnal species and a deliberate ambush predator, that settles in a coiled strike posture parallel to suitable rodent and small mammal runways. Both species are regularly encountered in degraded forest and habitat edges. Both species are arboreal, relatively abundant in the littoral forest fragments and tellingly, both are also reported from *Pandanus delphinensis* plants (Lehtinen, 2002). Relative to other forested areas, Sainte Luce supports a relatively depauperate carnivore community. *Cryptoprocta ferox* has not been observed in Sainte Luce now for over two decades (E.M. Ellis, pers. comm), but was reported in early faunal studies (Lewis Environmental Consultants, 1992b) and remains in the memory of community members. It is a known lemur predator and its broad diet certainly includes mouse lemurs (Hawkins and Racey, 2008). Its local disappearance is not well understood. However, the introduced predator *Felis catus* poses an increasing predation risk to *M. tanosi* in Sainte Luce, particularly in areas around human settlements and villages near to the forest edge. To what extent cats predate nocturnal lemurs in Sainte Luce is unknown, and although mouse lemurs are particularly agile and arboreal species, the capacity for cats to capture small mammalian prey is undeniable. In Sainte Luce, cats have on several occasions been observed predating the larger lemur species *Cheirogalues thomasi* (S. Hyde Roberts. pers. obs).

Table 3.

Candidate mouse lemur predators in Sainte Luce, their activity patterns and general diets. The list was populated from bird and herpetological surveys conducted by SHR since 2014 in addition with published studies (Lewis Environmental Consultants, 1992b; Goodman et al, 1997; Ellis, 2003; Ramanamanjato, 2008; Watson, 2008). *Cryptoprocta ferox has not been observed in Sainte Luce since the mid-1990s.

Class	Family	Genus	Species	Common Name	Activity Pattern	Diet
Aves	Accipitridae	*Accipiter*	*francesiae*	Frances's Sparrowhawk	Diurnal	Inverts and small vertebrates inc. small mammals
		Accipiter	*henstii*	Henst's Goshawk	Diurnal	Vertebrates inc. birds, small mammals and lemurs
		Accipiter	*madagascariensis*	Madagascan Sparrowhawk	Diurnal	Inverts and small vertebrates inc. birds
		Aviceda	*madagascariensis*	Madagascar Cuckoo-hawk	Crepuscular	Large invertebrates and small vertebrates inc. reptiles and frogs
		Buteo	*brachypterus*	Madagascar Buzzard	Diurnal	Inverts and small vertebrates inc frogs, small mammals and lemurs
		Milvus	*aegyptius parasitus*	Yellow-billed Kite	Diurnal	Carrion, inverts and small vertebrates
		Polybroides	*radiatus*	Madagascan Harrier-hawk	Diurnal	Large invertebrates and small mammals inc rodents and lemurs
	Falconidae	*Falco*	*concolor*	Sooty Falcon	Diurnal	Inverts and small vertebrates inc. birds
		Falco	*eleonorae*	Eleonora's Falcon	Diurnal	Inverts and small vertebrates inc. birds
		Falco	*newtoni*	Madagascar Kestrel	Crepsucular	Inverts and small vertebrates inc. frogs, small birds and small mammals
		Falco	*peregrinus*	Peregrine Falcon	Crepuscular	Small vertebrates but primarily birds
	Strigidae	*Asio*	*madagascariensis*	Madagascar Long-eared Owl	Nocturnal	Inverts and small vertebrates inc. small mammals and mouse lemurs
		Athene	*superciliaris*	White-browed Owl	Nocturnal	Inverts and small vertebrates
		Otus	*rutilus*	Madagascar Scops Owl	Nocturnal	Inverts and small vertebrates
	Vangidae	*Vanga*	*curvirostris*	Hook-billed Vanga	Diurnal	Inverts and small vertebrates such as frogs and chameleons
Reptilia	Boidae	*Sanzinia*	*madagascarciensis*	Madagascar Tree Boa	Nocturnal	Small mammals inc. rodents and mouse lemurs
	Lamprophiidae	*Ithychyphus*	*oursi*	—	Diurnal	Small vertebrates inc. chameleons, geckos, rodents and mouse lemurs
Mammalia	Eupleridae	*Cryptoprocta*	*ferox**	Fossa	Cathemeral	Carnivorous. Broad diet inc. inverts, reptiles, birds, lemurs and mouse lemurs.
	Felidae	*Felis*	*catus*	Domesticated cat	Nocturnal	Inverts and small vertebrates inc. snakes, lizards rodents and lemurs
	Hominidae	*Homo*	*sapien*	Human	Diurnal	Omnivorous

Finally, *M. tanosi* along with each of the other three species of lemur in Sainte Luce, is part of the human diet. Evidence of human lemur predation (e.g. snares, skewers and processed trees) in both the protected and unprotected forests has been observed in recent years. To what extent people actively hunt nocturnal lemurs in the area is unclear and the practice appears relatively covert. However, during an environmental education class conducted by SEED Madagascar in Ambandrika school in October 2017, roughly 60% of the 80 or so children (class sizes are dynamic, with most attendees aged between 8-16 years old) reported to having eaten lemur. However, there is some confusion surrounding the distinction between mouse lemurs and other lemur species. This startling figure suggests that the level of lemur consumption by the local community is high in Sainte Luce. This evidence has been further corroborated during recent household interviews conducted by E. Racevska (unpublished data collected 2019), and separately by SEED Madagascar (Project Oratsimba internal report, 2019). Both confirm that bushmeat consumption (including lemur) occurs throughout Sainte Luce, however levels appear to be much lower than the crude school assessment suggested, with just 6% of 120 surveyed households reportedly having consumed bushmeat.

Botanical assessment

This project included several elements requiring botanical assessment, with some aspects important for multiple chapters (e.g. identifying nest and sleeping sites, the determination of food species and as part of forest density measurements). Methods specific to particular chapter elements are covered in the methods sections of each respective chapter. Obtaining reliable scientific binomial names from local vernacular names is a significant challenge in the littoral forests. Fortunately, many men in the Sainte Luce area possess excellent local ecological knowledge and consensus on vernacular names was straightforward, with the experienced SEED Madagascar nursery manager (Lambo Johnarsson) able to validate the species names obtained by our local guides throughout the study. All scientific names were then obtained by cross-referencing vernacular names with a number of published sources (Bosser and Rabehevitra, 1996; Bollen, 2002; Lahann, 2006; Randriatafika and Rabenantoandro, 2007) and from a wider herbarium collection made by SHR and donated to Kew Gardens (Madagascar). Identifications were made by Dr David Rabevohitra at Kew in Antananarivo using the sample collection and an accompanying photographic collection. Finally, a small number of difficult samples were identified by Richard Razakamalala of Missouri Botanical Gardens (MBG) directly from collected samples and photographs. A complete list of tree species identified is provided in the **Appendix** (**Table 2**).

Ethics and permissions

All work undertaken throughout the duration of this study was conducted with the necessary permissions obtained through the Malagasy *Ministry of Environment, Ecology and Forestry* (MEEF), approved by the 'Directeur du Systeme des Aires Protegees', Antananarivo, Madagascar. All methods and protocols outlined herein were first considered and passed by the projects supervisory team at Oxford Brookes University (OBU) (Department of Social Sciences) in the United Kingdom and then accepted by the collaborating institution l'Université d' Antananarivo, Mention Zoologie et Biodiversite Animale (MZBA), Antananarivo, Madagascar. No ethical approval was deemed necessary by the University Research Ethics Committee (UREC) at OBU as no human participants were involved in the study. At a local level all methods were approved by NAP d' Ambatoantsiagnana area managers, QIT Madagascar Minerals and their environmental consultants 'Tropical Biodiversity and Social Enterprise' (TBSE). Final acceptance was then granted by the local 'Chef de Fokontany' (village leader) in Sainte Luce. Additional work in Nahampoana Private Reserve was undertaken on invitation from reserve management mediated through Air Fort Services, Tôlanaro, Madagascar. The Code of Best Practices for Field Primatology was consulted and used throughout the study (IPS, 2014). All work was carried out in adherence with the permissions set out in the following research permits; No.195/16/MEEF/SG/DGF/DSAP/SCB.Re, No.142/17/MEEF/SG/DGF/DSAP/SCB.Re (renewal) and No.260/18/MEEF/SG/DGF/DSAP/SCB.Re (renewal). Early trapping work was conducted under permit No.043/15/MEEF/SG/DGF/DSAP/SCB. Exported materials were licenced under Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) permits No.960C-EA11/MG17 and No.958C-EA12/MG19 and imported into the European Union under (CITES) permits No.565451/01 and No.585892/01. Copies of all permits are provided in the **Appendix** (**Permissions**).

Project collaborators

This project is the result of collaboration between the Department of Social Sciences at Oxford Brookes University in the United Kingdom and the Department of Animal Biology at the University of Antananarivo, Madagascar. In addition, the project represents a nascent collaboration between Oxford Brookes University and the UK based Non-Governmental Organisation (NGO) SEED (*Sustainable Environment, Education and Development*) Madagascar. In the first instance, the collaboration provided essential administrative support and facilitated the acquisition of necessary research permits, whilst SEED Madagascar provided invaluable in country support, field provisions and logistical aid. Both parties are committed to the in-situ and ex-situ research and conservation of the flora and fauna of Madagascar, and each provided particular expertise that benefitted this project.

CHAPTER 3

Morphological characterisation of *Microcebus tanosi*

Background

A species' evolutionary history is reflected in both its anatomy and behavioural ecology (Gebo, 2014), with both shaped by a long evolutionary history of adaptation, progressively augmenting survival ability, and each continually modulated by the environment (Darwin, 1859; Anthes et al, 2010; Nielsen, 2012). A species therefore represents a true time capsule, its ancestral past indelibly encoded into its morphology and behaviour as well as its genome. Understanding such adaptation can therefore provide insight into past evolutionary processes, reveal invisible environmental forces and can help to predict how biological communities might develop and adapt to change. Perhaps the most striking morphological feature of any species is its size. Body size is an important characteristic, essentially governing the ecological niche of a species, and placing fundamental constraints on integral life history traits such as diet and metabolism, locomotion and ranging behaviour, reproductive strategy and activity pattern (Jungers, 2013; Gebo, 2014; Kardong, 2018).

In general, extant species belonging to the order Primates exhibit a diverse range of overall body sizes, ranging from more than 200kg in adult male western gorillas (*Gorilla gorilla*) to just ~30g in adult Madame Berthe's mouse lemur (*Microcebus berthae*). The fossil record further elucidates this great range of body sizes, revealing tiny haplorhines from eastern China, estimated to weigh just 10-15g (Gebo et al, 2012; Gebo et al, 2017), to the extremely heavily bodied *Gigantopithecus,* an ape estimated to weigh as much as 400kg (Gebo, 2014). Despite this great diversity, extant species, along with some early ancestral fossil communities, are notably skewed towards smaller-sized taxa, mostly weighing below 5kg. Examination of the order also reveals a few other broad but interesting trends, with arboreal and nocturnal species being smaller than terrestrial and diurnal species, and strepsirrhines being in general smaller than haplorhines (Martin, 1990; Fleagle, 2013).

Today, the endemic primates of Madagascar, the Lemuriformes, illustrate these trends well. The largest extant lemur, the indri (*Indri indri*) weighs up to 9.5kg (Glander and Powzyk, 1998;

Mittermeier et al, 2010). However, the majority of lemurs are small bodied, nocturnal and belong to genera characterised by high levels of cryptic diversity (notably within *Microcebus Cheirogaleus* and *Lepilemur*). Archaeological evidence shows that much larger forms existed until very recently, with the largest (a sloth lemur, *Archaeoindris fontoynontii*) thought to weigh as much as 200kg (Jungers et al, 2008; Godfrey, 2016). It is now clear that the extinction of 8 genera and at least 17 species of 'giant lemur' mostly within the past 2,500 years (some within the past 500 years) has greatly diminished the range of anatomical and ecological adaptations now observable in Madagascar (Godfrey et al, 2004; Crowley et al, 2011; Goodman and Jungers, 2014) (**Fig. 16**). Analysis of sub-fossil remains obtained from excavation sites across the island, has revealed a final trend linked to body size, with each of the extinct lemur forms larger in size than the Indri. This interesting pattern of size dependent extinction has many implications for conservation biology and has led to multiple hypotheses to explain this phenomenon (Humbert, 1927; Godfrey and Jungers, 2003; Burney et al, 2004; Catlett et al, 2010; Mittermeier et al, 2010; Goodman and Jungers, 2014).

However, evolution shapes all aspects of a species morphology and behavioural ecology, with traits that experience the greatest selective forces i.e., have the most direct effect on survival, most adapted. Thus, the brain and associated sensory systems form an integral part of any adaptive complex (Barton et al, 2006) and on the whole represent overt adaptations within primates (Gebo, 2014), with primate brains enlarged relative to other mammal species. Sensory systems can also provide a proxy for how a lineage or taxon is adapted to a set of ecological pressures (Ali, 1978, Finlay and Sengelaub, 1981; Gebo, 2014). Furthermore, the size and sophistication of individual sensory structures within the brain are known to correspond with ecological patterns such as activity mode and diet (Barton et al, 2006, Dunbar and Schultz, 2007). As a result, it could be expected that the physical sensory apparatus associated with these relative brain developments would also show the most pronounced adaptations, particularly within nocturnal primate species (Endler, 1992; Jones, 1997; Boughman, 2002). Indeed, a substantial amount of evidence now exists that emphasises the importance of both chemical and aural communications (Niemitz, 1984; Zimmermann et al, 1988; Perret and Schilling, 1995; Zimmermann. 1995; Nietsch and Kopp, 1998; Anderson et al, 2000; Ambrose, 2003; Braune et al, 2008) in addition to the excellent vision maintained in nocturnal species (Bearder et al, 2006).

Figure 16 has been removed from this version of the thesis due to copyright restrictions

Figure 16 – Skull morphology of the living and extinct lemurs, representing the broad variation observable across the genera. Figure reproduced from Mittermeier et al, 2010. Drawings by S. D. Nash.

A period of great taxonomic expansion has characterised the past few decades of Primatology, particularly within the nocturnal lineages (Masters and Bragg, 1988; Martin, 1995; Bearder, 1999; Rasoloarison et al, 2000; Nekaris and Jaffe, 2007; Lei et al, 2014). However, much of the species-level diversity is highly cryptic in nature, with variation between congeneric species often barely discernible. The link between cryptic speciation and nocturnality has long been recognised (Patterson, 1985) and it has been postulated that a lack of visual communication coupled with the promotion of various other forms of con-specific signalling can result in phenotypic stasis (Heckman, 2006; Bickford et al, 2007). Such alternative means of communication do not necessarily require obvious physical adaptations and may instead result in subtle adaptations not easily detectable by biologists (Jones, 1997). It is now clear for example that acoustic signalling is phylogenetically relevant (Zimmermann et al, 2000; Méndez-Cárdenas et al, 2008) and differentiated mating calls can evolve very quickly in some genera (e.g. *Microcebus*), potentially providing important mechanisms for rapid speciation within isolated populations (Zimmermann and Hafen, 2001). Yet, it cannot be ignored that much of the early work that has led to our modern understanding of primate taxonomy was based on detailed study of morphological characteristics and behavioural ecology (Bearder et al, 1995; Anderson, 1998; Anderson et al, 2000; Rasoloarison et al, 2000; Nekaris and Jaffe, 2007), with modern genetic techniques providing a powerful, but relatively recent means of study. Unfortunately, however, the complementary morphological and ecological data accompanying many of the newly recognised species is often very limited and few modern comparative studies exist.

Mouse lemurs (genus *Microcebus*) are the world's smallest primates and today constitute one of the most speciose primate groups. They represent a radiation of small nocturnal cheirogaleids that are distributed widely throughout the forested habitats of Madagascar (Mittermeier et al, 2010). Mouse lemurs vary relatively little in terms of morphology and size, and species are superficially similar (Mittermeier et al, 2010). The basal origin of the radiation is estimated to have appeared in the order of 9-10mya (Yang and Yoder, 2003; Thiele et al, 2013), prompting the question as to how so many species could have evolved so rapidly, whilst barely seeming to have diversified at all, yet maintain species distinctiveness in areas of overlap? However, an emerging body of evidence, mostly gleaned from focused studies on sympatric species' pairs is now beginning to demonstrate that definite, but often highly subtle ecological, morphological and phenotypical differences do exist between species (Schmid and Kappeler, 1994; Rasoloarison et al, 2000; Rendigs et al, 2003; Radespiel et al, 2003b; Kobbe et al, 2011; Rakotondranary et al, 2011; Thoren et al, 2011; Dammhahn and Kappeler, 2014).

Given the phenotypic similarity between mouse lemur species, coupled with their small, nocturnal, arboreal and highly agile nature, it is easy to understand why such slight morphological traits and almost invisible ecological differences were not identified sooner. Indeed, the first intimation that hidden species may exist within the genus, beyond the two distinctly coloured lineages (Martin, 1972), came during a biometric study of two sympatric species, now known to represent both the largest and smallest forms (*M. murinus* and *M. berthae*) (Schmid and Kappeler, 1994). The fact that these two relatively extreme forms overlapped and were recognised provided an early signal for further research, and already prior to the advent of accessible genetic tools in the mid 2000s, a total of eight species had been recognised (Rasoloarison et al, 2000). Based solely on morphological evidence, these discoveries hinted at the prospect of a large and hitherto unknown cryptic community of nocturnal lemurs and the rapid expansion of species discoveries to come. Today, 26 mouse lemur species are recognised, with further discoveries anticipated as wider areas are explored, and genetic analysis reveals finer phylogenetic structuring (Sgarlata et al, 2019; Alexio-Pais et al, 2019; Schüßler et al, 2020).

Despite the proven utility of morphological analysis to reveal hidden species (Anderson, 1988; Schimd and Kapperler, 1994; Bearder, 1999; Masters and Bragg, 2000; Rasoloarison et al, 2000; Nekaris and Jaffe, 2007) and answer explicit questions related to behavioural ecology and the effect of environment (Darwin, 1859), the technique has now been supplanted as the primary method for classifying species. The continual development of genetic techniques and their ability to expose hidden diversity, demarcate species boundaries and resolve contentious phylogenetic relationships has proven immensely powerful and time effective (in mouse lemurs alone: Heckman et al, 2006; Louis et al, 2006; Olivieri et al, 2007; Radespiel et al, 2008; Radespiel et al, 2012; Rasoloarison et al, 2013; Hotaling et al, 2017; Sgarlata et al, 2019). However, not only do anatomical and ecological studies corroborate species delimitation, they provide a tangible representation of evolutionary processes and reveal the range of expressed adaptations. As a result of the rapid expansion in recognised mouse lemur species, the majority of newly described forms are based largely, if not exclusively on mitochondrial DNA analysis, and often from only a limited number of samples (Markolf et al, 2011). *Microcebus tanosi* represents one of the most recently described species (Rasoloarison et a, 2013), whose description, based largely on mtDNA evidence and biometric measurements, relied on such a small collection of individuals (n=10).

Today, *M. tanosi* is known to occupy the low altitude rainforests of the Vohimena and Anosyenne mountains, the littoral forests of Sainte Luce and several relict inland forests, with several sub-populations now isolated from one another. In light of our ever-improving distributional and

taxonomic understanding, a number of earlier published works, some certainly involving *M. tanosi*, can be re-evaluated (Lewis Environmental Consultants, 1992b; Andrianasolo et al, 2006; Ganzhorn et al, 2007; Hapke et al, 2011, Rakotondranary et al, 2011; Hapke et al, 2012, Nguyen et al, 2013; Sommer et al, 2014). Fortunately, in most cases species identity is relatively simple to interpret as many of the studies include genetic components. New interpretations of the literature allow for a series of comparative investigations and provide a collection of useful data that can be re-purposed to answer new questions. To date, the morphological plasticity of mouse lemurs has received relatively little attention and by synthesising published works and novel data, a comparative study of biometric and phenotypic divergence between populations is possible.

In this chapter I present a series of biometric data for *M. tanosi* obtained from the littoral forests of Sainte Luce and the botanical arboretum at Nahampoana Private Reserve and provide a comparison of sub-populations based on a series of morphological traits. At the outset of this study, it was unclear whether a single species of mouse lemur or a sympatric species pair occupied the littoral forests of Sainte Luce, whilst the identity of the species at Nahampoana was entirely unknown. Species validation presented a crucial initial step and provided the foundation for subsequent work. This chapter also includes supplementary data gathered from both published and unpublished sources, from genetically confirmed populations across the species range, enabling the further comparison of biometric traits across four isolated populations. The chapter also outlines the results of the capture process along with basic reproductive descriptives, such as inferred breeding schedule, gross reproductive morphology and proposes a new framework for classifying age classes based on weight. Such traits may serve to further separate *M. tanosi* ecologically from other phylogenetically and geographically proximal mouse lemur species and provide an indication of how environmental factors may be influencing life history traits. The data provide some utility for future studies and provide a foundation for future inter and intra species comparative work. In order to frame this data properly, the following chapter will address the following questions:

1) Do the forests of Sainte Luce and Nahampoana support a single species of *Microcebus* or sympatric species pairs, and what are their identities?
2) What are the morphological parameters that define *M. tanosi* across its known range?
3) Do isolated populations of *M. tanosi* show any discernible morphological variation?
4) What natural history traits can be derived from the dataset and the capture data?

Based on the provisional hypotheses:

1) The littoral forests of Sainte Luce support a single species of Microcebus, based on phenotype and repeated observation. In contrast, Nahampoana Private Reserve likely represents a contact zone between *M. tanosi* and *M. ganzhorni* and species occupancy is unknown.
2) *Microcebus tanosi* will closely resemble other eastern *Microcebus* forms in terms of general morphology, in line with the original species description.
3) Little intra-specific variation is anticipated between the isolated populations, despite occupying differentiated and isolated forest habitats, given that relatively little variation exists between eastern species.
4) *Microcebus tanosi* will share the strict seasonal reproductive schedule of other mouse lemurs, along with the associated morphological characteristics. Similarly, no sexual dimorphism is expected.

Methodology

Mouse lemurs were captured by means of Sherman trapping and direct capture (**Chapter 2**, **Trapping and capture methodology**). Traps were deployed in Sainte Luce between April 2015 and May 2019, across five trapping periods (April-October 2015, September-November 2016, August 2017, August-October 2018 and May 2019). Prior to trapping, it was unknown whether the target species displayed any habitat preference (e.g. forest edge or forest interior), so traps were deployed based on the assumption that animals could be captured with equal success across a range of habitats types (e.g. areas with specific characteristics) in three forest fragments (S7, S8 and S9) (**Fig. 17**). Baited traps (banana) were deployed in sets of 20 per locality, with traps set in pairs and positioned at approximately 10m apart. Traps were freshly baited and opened each evening for a period of four consecutive nights. No trapping took place between January and March, a period when the trapping success of mouse lemurs was shown to be at its minimum in the nearby littoral forests of Mandena (Lahann et al, 2006). Trapping was supplemented by direct capture in Sainte Luce. Similarly, all individuals at Nahampoana Private Reserve were captured by hand on the nights of 27 May 2019 and 08 June 2019.

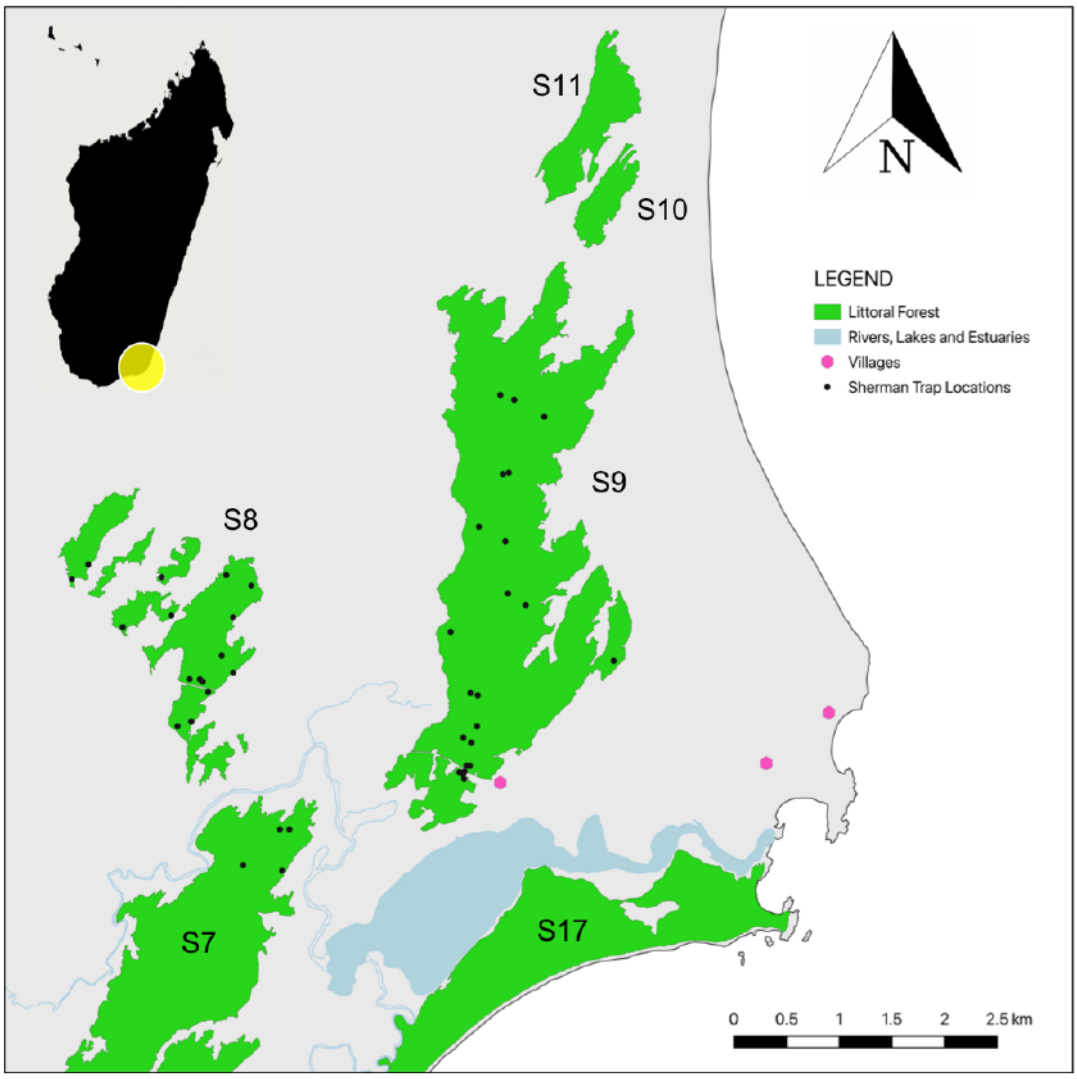

Figure 17 – The location of 42 Sherman trapping sites in the littoral forest fragments of Sainte Luce. Traps were set in S7 (n=4), S8 (n=16) and S9 (22).

All animals captured in Sainte Luce were measured at the SEED Madagascar research centre, and those in Nahampoana at the field reserve. A suite of characteristics and biometric measurements were recorded for each individual mouse lemur, with 38 morphological traits recorded for each male and 35 for females (additional reproductive measurements recorded in males). A description of each relevant measurement is provided below (**Table 4**). Measurements were taken in accordance with Haffen et al. (1998), Masters and Bragg (2000) and Rasoloarison et al. (2000) and in line with Groves and Harding (2003) and Rakotondranary et al. (2011). Head and limb measurements provide approximations of both skull and bone lengths (McArdle, 1981). Inter-membranal, Crural and Brachial indices were calculated based on the relative lengths of the limbs of adult individuals, providing a species-specific index of locomotive mode.

Table 4.

The biometric characters recorded for each *M. tanosi* individual captured at Sainte Luce and Nahampoana Private Reserve. All measurements recorded using a digital calliper and recorded to the nearest millimetre. Mass measurements were recorded using a calibrated spring Pesola and weighed to the nearest ±0.5gram. All measurements taken under the supervision of SHR.

Measurement	Description
Body mass	weighed using a calibrated Pesola, to the nearest ±0.5g.
Body mass index	mass (kg) / [body length (m)]^2
Head and body length	tip of the nose to the distal most point of the body (base of the tail).
Tail length	base of the tail to the end of the most distal vertebrae, excluding terminal hair tufts.
Tail width	diameter of tail at closest point to body.
Total length	head and body length plus tail length.
Dorsal stripe length	the full length of the visible dark dorsal pelage stripe.
Dorsal stripe width	the width of the visible dark dorsal stripe at midbody.
Head length	distance between the nostrils and foramen magnum.
Head width	bizygomatic distance perpendicular to head length.
Ear length	measured from the distal most tip of the pinna, to the basal notch.
Ear width	maximum width measured perpendicular to the ear length.
Nasal stripe length	extent of visible white inter-ocular stripe from nose to forehead.
Nasal stripe width	extent of visible white inter-ocular stripe perpendicular to stripe length.
Eye diameter	maximal width of eye orbits, from distal edges of the zygomatic arches.
Canine length	length of canine measured from gumline to crown tip.
Internarial distance	distance between nostrils.
Humerus length	greatest length of the humerus bone in relation to the shaft.
Radius length	greatest length of the radial bone in relation to the shaft.
Femur length	greatest length of the femur bone in relation to the shaft.
Tibia length	greatest length of the tibia bone in relation to the shaft.
Hind foot length	from the back edge of the heel to the tip of the longest toe (excluding nail).
Hind foot width	perpendicular width of foot in relation to hind foot length.
Toe length	the full extent of the longest toe, from proximal metatarsal to tip (excluding nail).
Hand length	from the distal edge of the wrist to the tip of the longest finger (excluding nail).
Hand width	perpendicular width of palm in relation to hand length.
Finger length	full extent of the longest finger, from proximal phalange to tip (excluding nail).
Testes length	proximal to distal length of testes in males.
Tested width	perpendicular width in relation to testes length. Both testes measured separately.
Intermembranal Index	(humerus + radius) / (femur + tibia) x 100
Crural Index	tibia length x 100 / femur length
Brachial Index	radial length x 100 / humerus length

During the measuring procedure, the age class of each individual was determined based on definitions provided by Groves and Harding (2003) (**Table 5**). The sexual characteristics of each individual were examined, primarily in order to determine sex, but also to establish reproductive status. Many male primates, especially strepsirrhines, are known to exhibit marked changes in testicular size in accordance with breeding condition, and mouse lemurs are a prominent example

(Wrogemann et al, 2001). For male individuals, both length and width of the testes were measured with digital callipers, and testicular volume was calculated using the following equation (as in a regular ellipsoid):

$$TV = [\pi \times (width)^2 \times length] / 6$$

For female individuals, examination included an assessment of both the vulva and nipple condition (Radespiel et al, 1998; Wrogemann et al, 2001). Both characteristics may indicate reproductive activity. Sexual swelling was noted along with any obvious signs of pregnancy, assessed by means of abdominal palpation. Nipples can become enlarged and elongated during the weaning of young, and examination can signal whether a female has recently given birth and is suckling neonates or infants. Given that mouse lemurs can become sexually active within their first year, any developed individuals captured after August may be considered as sexually active. As a result, both adults and sub-adults combined constitute the breeding population of the species.

Table 5.

Definitions of maturity status classification used in the following chapter. Adapted from Groves and Harding in Setchell and Curtis (Eds) 2003.

Age Class	Definition
Neonate	Infant showing signs of having been very recently born (a few days)
Infant	Unweaned; not independently moving (carried about, in nest, etc.)
Juvenile	Immature but independently moving
Immature	Any individual not evidently sexually mature
Sub-adult	Individual that is apparently sexually mature, but not physically mature.
Adult	Both sexually and physically mature
Mature Adult	Adult showing apparent signs of age degeneration

In order to fully characterise *M. tanosi*, the biometric data collected in this study from Sainte Luce and Nahampoana (see **Appendix**; **Table 3a+3b**) is supplemented with data obtained from both published (Rakotondranary et al, 2010 and Rasoloarison et al, 2015) and unpublished sources. Unpublished data is provided by Dr A. Hapke and N. Andrianjaka from Ivolo and Enato, collected between November and December 2009 (n=17); by Dr E. Louis, collected from Ampasy in

October 2015 (n=2) and by Prof. P. Wright, collected near Ivohibory (the Lost Rainforest) in October 2016 and November 2019 (n=10) (see **Chapter 2**, **Figure 13**). Although in some cases datasets are limited and some preclude raw data analysis, together they provide an overall image of the species' biometric character across its known range. A total of ten shared morphometric measurements are presented. Statistical comparison was restricted to just the four populations for which sufficient raw data is available; Sainte Luce, Nahampoana, Ivolo and the Lost Rainforest, and the biometric traits common to each dataset; mass, total length, body length, tail length, ear length and foot length. The timing of each of the studies is an important consideration and likely reflects the developmental profile of the sample community. Respective individuals captured by Rasoloarison et al (2015), including the type specimen were captured in April 2007 and those from Rakotondranary et al (2010) were captured between April and June 2006 - 2009. All individuals in this study from Nahampoana Private Reserve were captured between May and June 2019, and those from Sainte Luce between the months of August to November, 2015-2019. Each dataset includes both adults and sub-adults.

Statistical analysis was performed using IBM SPSS Statistics version 26. 2-Independent sample non-parametric tests (Mann-Whitney U) were used to directly compare between the Sainte Luce and Nahampoana populations and to compare traits between sexes. Adult and sub-adult individuals were pooled for each population. Between population trait analysis based on five shared biometric characteristics was carried out using Kruskal-Wallis tests. Pairwise comparisons were adjusted using the Bonferroni correction for multiple tests. Significance level was set at 0.05. A Discriminant Function Analysis was performed on the four population datasets to assess trait separation between groups and to determine intra-species variation, again based on five common non-correlated characteristics (mass, body length, tail length, ear length and foot length).

Each individual animal captured during this study was first identified to species level in the field based on morphology and phenotype, and later confirmed by genetic analysis. A series of hair and tissue samples were collected from each individual as part of the standard processing protocol (**Chapter 2**, **Animal processing)**. For each mouse lemur captured, an ear biopsy was taken, and a series of hairs were extracted (minimum of 20 follicles per individual). Tissue samples were stored in 95% $EtOH^2$ and hair samples were dry stored in hermetic eppendorf tubes. Species identify was confirmed with microsatellite analysis, performed by Dr Christian Roos at the German Primate Centre (DPZ - Deutsches Primatenzentrum). All mouse lemur individuals were genotyped at 1 mitochondrial locus – the hypervariable region 1 (HV1) of the control region (C. Roos. pers. comm). The same procedure was also followed for other non-primate captures.

Results

Trapping

A total of 3,360 trap nights across three littoral forest fragments resulted in the capture of 165 animals. Catches comprised of four species, with two species of rodent (1 endemic species and 1 invasive) and two species of lemur represented. Of all captures, 62.42% (103 individuals) were identified in the field as *Rattus rattus*, 30.90% (51 individuals) were identified as *Eliurus webbi*, 4.24% (7 individuals) were identified as *Microcebus tanosi* and 2.42% (4 individuals) as *Cheirogaleus thomasi* (**Table 6**). Trapping success was low across the capture period (April – December), with mouse lemurs only captured in August (n=1) and September (n=6). Capture success reached a maximum in September at just 0.54%. Three mouse lemur individuals were captured in forest fragment S8 and four in S9. Of these, six were female (5 adults and 1 sub-adult) and just one was male (sub-adult). No individuals were recaptured in over the study.

Direct capture

A further 45 mouse lemurs were captured using direct methods (Sainte Luce n=35, Nahampoana n=10) between October 2016 and June 2019. A summary of sex and age class at each location is provided in **Table 7**. Of those captured in Sainte Luce, three were captured in forest fragment S7, four in S8 and 28 were captured in S9. Average direct capture success rates were 13.1% in Sainte Luce and 32.3% at Nahampoana.

Genetic results

All individual mouse lemurs captured in this study were genotyped (Sainte Luce n=42; Nahampoana n=10) and confirmed as *Microcebus tanosi*. The identity of the other species captured was also assessed, with initial field designations confirmed in all cases. All species were already known to inhabit each of the study fragments in Sainte Luce, but identity was uncertain.

Maturity classes

The maturity statuses assigned to each individual mouse lemur based on appearance and general character corresponded neatly with body mass categories. Body mass therefore confirmed initial age classes assessment. Mass categories serve adequately for both sexes. In this study all mature individuals (likely +2 years old) weighed +60g, individuals deemed as sub-adults (likely between nine months to two years old) ranged between 40-59.9g, juvenile individuals ranged between 15g and 39.9g and infants below 15g. A full description of each population of *M. tanosi* in this study is provided in **Table 9** (and see **Appendix**; **Table 3a+3b**).

Table 6.

Sherman trap capture success (%) for each species trapped in the study, combing monthly data across the sampling years. No traps were deployed in January, February or March. Number of individual captures per species in parenthesis. *Total trap success is adjusted for *Cheirogaleus thomasi* as the species hibernates during the cooler winter months (May-September).

Month	Trap Nights	*M. tanosi*	*C. thomasi*	*E. webbi*	*R. rattus*	Total
Apr	160	0.00	0.00	0.00	1.88 (3)	1.88
May	240	0.00	0.00	1.67 (4)	2.50 (6)	4.17
Jun	80	0.00	0.00	0.00	3.75 (3)	3.75
Jul	80	0.00	0.00	3.75 (3)	0.00	3.75
Aug	560	0.18 (1)	0.00	1.43 (8)	2.50 (14)	4.11
Sep	1120	0.54 (6)	0.00	2.41 (27)	3.66 (41)	6.61
Oct	720	0.00	0.14 (1)	1.11 (8)	2.08 (15)	2.78
Nov	320	0.00	0.94 (3)	0.31 (1)	6.56 (21)	7.81
Dec	80	0.00	0.00	0.00	0.00	0.00
Total	3360	0.21 (7)	0.31* (4)	1.52 (51)	3.07 (103)	

Table 7.

Demographic summary of all mouse lemurs captured by in Sainte Luce and Nahampoana. *Indicates additional juvenile whose sex could not be determined. A further two animals captured in Sainte Luce were classified as infants and could not be sexed (not included in table).

Locality	Sex	Maturity Status		
		Juvenile	Sub-adult	Adult
Sainte Luce (n=42)	Male	–	4	7
	Female	4	10	14
	Total	5*	14	21
Nahampoana (n=10)	Male	–	–	1
	Female	2	5	2
	Total	2	5	3
Total (n=52)	Male (n=11)	–	4	8
	Female (n=32)	6	15	16

Inter-site comparison: Sainte Luce vs Nahampoana

A total of 20 biometric traits were compared between the two datasets. Six biometric characteristics showed statistically significant divergence: total length (U=65.000, p=0.022, n=43), body length (U=60.000, p=0.013, n=43), tail width (U=71.500, p=0.032, n=43), foot length (U=76.500, p=0.047, n=43), head width (U=105.000, p=0.012, n=39) and femur length

(U=54.000, p=0.022, n=37) (**Table 8**). Divergent traits appear to be related to size (tail length also shows a trend towards significant divergence; U=87.000, p=0.098, n=43) rather than those linked to sensory perception (ear dimensions, eye diameter) or locomotion (intermembranal, crural and brachial indices). Features recorded in the smaller sampled population (Nahampoana) are largely within the parameters of the larger sample set (Sainte Luce).

Table 8.

Mean values and standard deviations of traits that differ significantly between individuals captured at Sainte Luce and Nahampoana Private Reserve. All measurements obtained at Nahampoana were recorded in May and June 2019, whilst measurements from Sainte Luce were collected between September 2015 and May 2019.

Locality	Statistic	Biometric Traits					
		TTL (mm)	BL (mm)	TW (mm)	Head W (mm)	Femur (mm)	FL (mm)
Sainte Luce (n=35)	Mean	258.79	128.04	9.62	24.57	32.89	13.29
	SD	±18.55	±10.06	±1.97	±2.48	±5.17	±1.47
Nahampoana (n=8)	Mean	242.00	117.75	8.00	21.96	28.57	12.20
	SD	±20.25	±11.82	±1.53	±2.12	±2.77	±1.66

Intra-specific variation: Comparison of four populations

An overview of the full biometric character of *M. tanosi* is provided in **Table 9**. Overall significant intra-specific differences were found between the four populations (Sainte Luce, Nahamapoana, Ivolo and the Lost Rainforest) across traits; total length (Kruskal-Wallis test=17.115, df=3, p=0.001, n=68), body length (KWt=19.738, df=3, p=<0.001, n=68), tail length (KWt=26.904, df=3, p=<0.001, n=68), ear length (KWt=28.703, df=3, p=<0.001, n=68) and foot length (KWt=36.070, df=3, p=<0.001, n=68), whereas body mass also showed a trend towards significance (KWt=6.817, df=3, p=0.078, n=68). Results of significant pairwise comparisons and comparative trait directionality are presented in **Table 10.**

Table 9.

Descriptive summary of all known *Microcebus tanosi* populations. Data obtained from published data sources and personal communications. In each case, both sub-adult and adult individuals are combined to give a more balanced and overall characterisation of each breeding population. *Refers to type specimen. Note that the low mass records in Rakotondranary et al, 2010 possibly indicates the inclusion of immature / juvenile individuals.

Locality	Sainte Luce (n=35)				Nahampoana (n=8)				Mahamavo (n=17)				Manantantely + Ivohibe (n=4)			
	This study				This study				Rakotondranary et al, 2010				Rasoloarison et al, 2013			
Trait	*n*	Min	Max	Mean ± SD	*n*	Min	Max	Mean ± SD	*n*	Min	Max	Mean ± SD	*n*	Min	Max	Mean ± SD
Body mass (sexes combined)	35	41.0	78.5	60.1 ± 9.6	8	41.5	73.6	55.5 ± 10.4	17	35.0	72.0	45.1 ± 10.2	4	48.0	60.0	51.5 ± 5.7
Body mass (female)	24	41.0	78.5	59.4 ± 10.2	7	41.5	73.6	54.5 ± 10.8	9	35.0	72.0	46.7 ± 12.8	1*	49.0	49.0	NA
Body mass (male)	11	47.0	72.0	61.6 ± 8.7	1	62.4	62.4	NA	8	37.0	56.0	43.3 ± 6.3	-	NA	NA	NA
Total length (sexes combined)	35	234.0	298.5	258.8 ± 18.5	8	214.0	275.0	242.0 ± 20.2	17	-	-	257.0 ± 13.3	4	254.0	275.0	264.8 ± 11.8
Head and body length (sexes combined)	35	111.0	153.7	128.0 ± 10.1	8	109.0	139.0	117.8 ± 11.8	17	115.0	135.0	125.0 ± 5.3	4	116.0	140.0	126.5 ± 1.0
Head and body length (female)	24	111.0	153.7	126.1 ± 9.1	7	109.0	123.0	114.7 ± 8.8	9	120.0	130.0	125.0 ± 5.0	1*	125.0	125.0	NA
Head and body length (male)	11	113.5	150.3	132 ± 11.2	1	139.0	139.0	NA	8	115.0	135.0	125.0 ± 6.0	-	NA	NA	NA
Tail length	35	106.1	153.8	130.7 ± 11.0	8	110.0	145.0	124.3 ± 11.3	17	120.0	150.0	132.0 ± 8.0	4	115.0	150.0	138.8 ± 16.5
Head length	31	31.4	44.0	36.9 ± 2.7	8	31.9	39.9	35.6 ± 3.1	17	33.0	37.0	35.0 ± 1.0	-	NA	NA	NA
Head width	31	20.1	33.6	24.7 ± 2.9	8	19.2	24.8	21.6 ± 2.1	17	20.0	23.0	22.0 ± 1.0	-	NA	NA	NA
Ear length	32	11.2	18.1	14.3 ± 2.1	8	9.8	15.3	12.7 ± 1.8	17	17.0	19.0	18.0 ± 1.0	4	19.0	20.0	19.5 ± 0.3
Ear width	32	7.2	12.7	10.2 ± 1.1	8	7.7	12.1	10.3 ± 1.6	17	12.0	15.0	13.0 ± 1.0	-	NA	NA	NA
Tibia Length	29	20.0	38.1	29.2 ± 4.6	8	17.0	32.0	25.6 ± 4.9	17	36.0	41.0	38.0 ± 1.0	-	NA	NA	NA
Hind foot Length	35	18.8	29.4	24.7 ± 2.5	8	21.6	23.9	23.1 ± 1.8	17	30.0	33.0	32.0 ± 1.0	4	30.0	33.0	32.0 ± 1.4
Tail length / head length	31	2.8	4.1	3.6 ± 0.3	8	2.9	3.9	3.5 ± 0.3	17	3.5	4.2	3.8.0 ± 2.0	-	NA	NA	NA
Tail length / head width	31	3.7	7.1	5.3 ± 0.7	8	4.6	6.7	5.7 ± 0.8	17	5.5	6.7	6.1 ± 3.0	-	NA	NA	NA

Locality	Ampasy (n=?)				Ivolo + Enato (n=17)				Lost Rainforest (n=10)				All localities combined			
	Unpub. pers comm Dr. Ed Louis				Unpub. pers comm Dr. Andreas Hapke				Unpub. pers comm Prof. Patricia Wright							
Trait	*n*	Min	Max	Mean ± SD	*n*	Min	Max	Mean ± SD	*n*	Min	Max	Mean ± SD	*n*	Min	Max	Mean ± SD
Body mass (sexes combined)	-	-	-	-	17	47.0	81.0	66.4 ± 9.8	10	40.0	66.0	49.5 ± 8.7	91	35.0	81.0	54.7 ± 7.7
Body mass (female)	-	-	-	-	12	61.0	81.0	71.4 ± 6.0	6	40.0	55.0	48.1 ± 8.4	59	35.0	81.0	56.0 ± 10.0
Body mass (male)	-	-	-	-	5	47.0	61.0	54.4 ± 5.8	4	43.0	66.0	51.7 ± 10.1	29	37.0	72.0	54.7 ± 7.8
Total length (sexes combined)	-	-	-	-	17	251.0	285.0	267.1 ± 10.8	10	219.0	268.0	240.0 ± 14.6	91	214.0	298.0	255.0 ± 11.4
Head and body length (sexes combined)	-	-	-	-	17	109.8	131.4	117.9 ± 6.7	10	106.0	130.0	114.8 ± 6.0	91	109.0	153.7	121.7 ± 5.5
Head and body length (female)	-	-	-	-	12	111.0	131.4	119.6 ± 7.2	6	106.0	130.0	116.8 ± 9.0	59	106.0	153.7	120.4 ± 5.0
Head and body length (male)	-	-	-	-	5	109.8	117.3	114.0 ± 2.9	4	108.0	122.0	115.5 ± 6.0	29	108.0	150.3	125. 1 ± 10.7
Tail length	-	-	-	-	17	139.0	169.0	147.0 ± 0.8	10	105.0	143.0	123.5 ± 11.8	91	105.0	169.0	132.7 ± 9.0
Head length	-	-	-	-	17	34.3	37.6	36.1 ± 1.0	-	NA	NA	NA	73	31.4	44.0	35.9 ± 0.8
Head width	-	-	-	-	17	21.3	23.4	22.1 ± 0.7	-	NA	NA	NA	73	19.2	33.6	22.6 ± 1.4
Ear length	-	-	-	-	17	17.4	19.1	18.2 ± 0.5	10	11.0	19.0	14.3 ± 3.5	88	9.8	19.1	16.2 ± 2.7
Ear width	-	-	-	-	17	11.7	14.7	13.2 ± 0.8	-	NA	NA	NA	74	7.2	15.0	11.7 ± 1.6
Tibia Length	-	-	-	-	-	NA	NA	NA	-	NA	NA	NA	54	20.0	41.0	30.9 ± 6.4
Hind foot Length	-	-	-	-	17	32.0	34.0	33.41 ± 0.7	10	15.0	29.0	25.9 ± 4.1	74	15.0	33.0	27.5 ± 4.2
Tail length / head length	-	-	-	-	17	3.7	4.7	4.1 ± 0.2	-	NA	NA	NA	73	2.8	4.7	3.8 ± 0.3
Tail length / head width	-	-	-	-	17	6.5	7.8	6.7 ± 0.4	-	NA	NA	NA	73	3.7	7.8	6.0 ± 0.6

Table 10.

Significant pairwise comparisons between the five shared significant traits common to the four isolated populations of *Microcebus tanosi* at Sainte Luce (SL), Nahampoana Private Reserve (Nah), Ivolo (Ivo) and Ivohibory or the Lost Rainforest (LR). Significance values adjusted using the Bonferroni correction for multiple tests. *Indicates a trend towards significance.

Trait	n	Sub-population	Means + SD (mm)	Test Statistic	Adj. Sig[a]
Total length	45	SL - LR	258.8 ± 18.5 / 240.0 ± 14.6	−19.136	0.042
	23	Nah - Ivo	242.0 ± 20.2 / 267.1 ± 10.8	−25.796	0.017
	25	Ivo - LR	267.1 ± 10.8 / 240.0 ± 14.6	−28.783	0.002
Body length	43	SL - Nah	128.0 ± 10.1 / 117.8 ± 11.8	−19.877	0.062*
	50	SL - Ivo	128.0 ± 10.1 / 117.5 ± 6.2	−20.914	0.004
	45	SL - LR	128.0 ± 10.1 / 116.3 ± 7.6	−22.864	0.008
Tail length	50	SL - Ivo	130.7 ± 11.0 / 147.0 ± 0.8	−24.252	<0.001
	23	Nah - Ivo	124.3 ± 11.3 / 147.0 ± 0.8	−34.892	<0.001
	25	Ivo - LR	147.0 ± 0.8 / 123.5 ± 11.8	−35.217	<0.001
Ear length	50	SL - Ivo	14.3 ± 2.1 / 18.2 ± 0.5	−28.662	<0.001
	23	Nah - Ivo	12.7 ± 1.8 / 18.2 ± 0.5	−38.708	<0.001
	25	Ivo - LR	18.2 ± 0.5 / 14.3 ± 3.5	−27.383	0.004
Foot length	50	SL - Ivo	24.7 ± 2.5 / 33.4 ± 0.7	−25.138	<0.001
	45	SL - LR	24.7 ± 2.5 / 25.9 ± 4.1	−18.929	0.045
	23	Nah - Ivo	23.1 ± 1.8 / 33.4 ± 0.7	−36.954	<0.001
	25	Ivo - LR	33.4 ± 0.7 / 25.9 ± 4.1	−44.067	<0.001

A Discriminate Function Analysis was performed, based solely on the significantly divergent traits, in order to assess the likelihood that individuals could be grouped into the correct populations based on these characteristics. The first 2 canonical functions produced significant results with p-values of <0.001 and 0.001 (Function 1: Wilks' Lambda=0.307, X^2=74.349, df=12 and Function 2: Wilks' Lambda=0.684, X^2=23.924; df=6), indicating significant morphological difference between groups. The first canonical discriminant function accounts for 73.6% of variance, whilst function 2 accounts for 22.8%. The structure matrix revealed that the variance accounted for in function 1 is largely due to between groups variation in foot length (0.716), tail length (0.497) and ear length (0.501), whilst function 2 largely accounts for the between groups variation in body length (0.595). Foot length and tail length provide the largest absolute correlation between each variable and any discriminant function and provide the majority of the between population variance. **Figure 18** provides a visual representation of the separation of the different sub-populations.

Classification success for all individuals is 77.9%. Of the 68 individuals analysed, 85.7% of individuals from Sainte Luce were correctly assigned to the true population, just 25% of individuals were correctly assigned to the Nahampoana group, 100% of individuals were correctly assigned to the Ivolo group and 60% were correctly assigned to the Lost Rainforest group (**Table 11**). These results indicate considerable overlap between the populations, with individuals from Nahampoana appearing to be intermediate and most likely to be mis-classified. In contrast, individuals from Ivolo appear most distinctive.

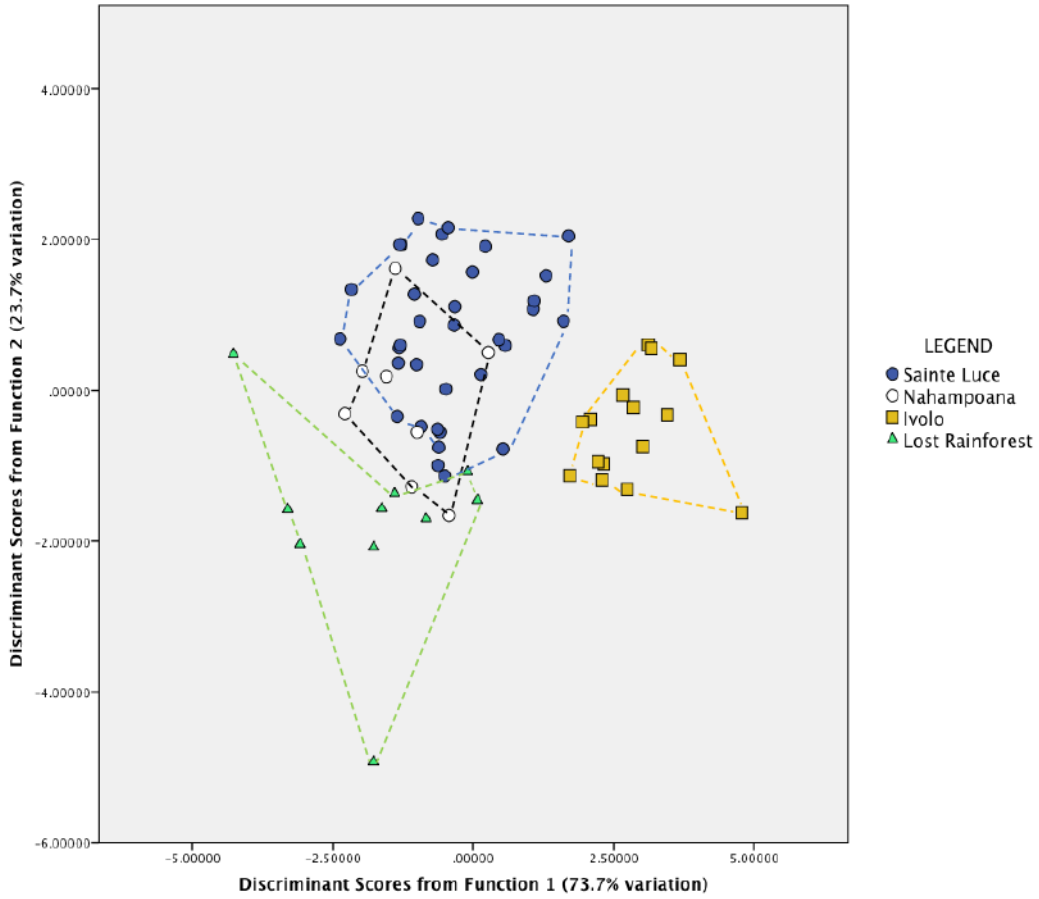

Figure 18 – Discriminate Function Analysis plot showing separation of each sub-population based on five shared morphological traits. Combined, functions 1+2 represent 97.4% of observed variation between groups. Function 1 (x axis) is largely derived from foot length, ear length and tail length, whilst function 2 (y axis) is predominantly based on body length. Positive Discriminant Scores reflect larger traits values.

Table 11.

Discriminate Function Analysis predicted group membership. Success of individual assignment to each population based on 6 biometric characteristics.

	Locality	Individual assignment to populations				
		Sainte Luce	Nahampoana	Ivolo	Ivohibory	Total
Count	Sainte Luce	30	0	1	4	35
	Nahampoana	4	2	1	1	8
	Ivolo	0	0	15	0	15
	Lost Rainforest	2	1	1	6	10
%	Sainte Luce	85.7	0	2.9	11.4	100
	Nahampoana	50	25	12.5	12.5	100
	Ivolo	0	0	100	0	100
	Lost Rainforest	20	10	10	60	100

Sexual dimorphism and inter-species comparison

The average body mass of reproductive individuals (sub-adult and adults combined) across the known range (**Table 9**) is 54.7g (n=91, SD±7.7g), with both sexes showing comparable weights (females; n=59, mass 56.0g, SD±10.0 and males; n=29, mass 54.7, SD±7.8). This study finds no evidence for sexual dimorphism in *M. tanosi* across six biometric traits (body mass U=476.500, p=0.821, n=68; total length U= 387.000, p=0.159, n=68; body length U=444.500, p=0.515, n=68; tail length U=375.000, p=0.116, n=68; ear length U=436.000, p=0.445, n=68 and foot length U=441.500, p=0.489, n=68). Average total body length for sexually mature individuals is 255.0mm (n=90, SD 14.5mm), with the largest individuals found at the rainforest site of Ivolo (267.1mm; n=17), and the smallest in the northernmost locality, the Lost Rainforest site (240.0mm; n=10). The largest animal measured in the study, an adult female captured in Sainte Luce measured 298.5mm, demonstrating that *M. tanosi* can reach large sizes comparable to other proximal and eastern mouse lemur species (**Tables 12**, **13a** and **13b)**.

Table 12.

Comparison of biometric traits; *M. tanosi* from Sainte Luce and Nahampoana Private Reserve with *M. ganzhorni* from Mandena (*Lahann et al, 2006). Data from Sainte Luce and Nahamapoana includes both adult and sub-adult individuals. Mandena is the type locality for *M. ganzhorni* yet is only 25km from Sainte Luce and just 1.25km from Nahampoana (see **Chapter 2**, **Species distribution**).

Trait	*M. tanosi* (Sainte Luce)	*M. tanosi* (Nahampoana)	*M. ganzhorni** (Mandena)
Total length (mm)	258.8 ± 18.5	242.0 ± 20.2	-
	(234.0 - 298.5; n=35)	(214 - 275; n=8)	-
Tail length (mm)	130.7 ± 11.0	124.3 ± 11.3	132.5 ± 7.4
	(106.1 - 153.8; n=35)	(110.0 - 145.0; n=8)	(n=127)
Head length (mm)	36.9 ± 2.7	35.6 ± 3.1	35.0 ± 1.2
	(31.4 - 44.0; n=31)	(31.9 - 39.9; n=8)	(n=127)
Head width (mm)	24.7 ± 2.9	21.6 ± 2.1	21.8 ± 1.3
	(20.1 - 33.6; n=31	(19.2 - 24.8; n=8)	(n=127)
Hind foot length (mm)	24.7 ± 2.5	23.1 ± 1.8	32.4 ± 1.4
	(18.8 - 29.4; n=35)	(21.6 - 23.9; n=8)	(n=127)
Ear Length (mm)	14.3 ± 2.1	12.7 ± 1.8	23.5 ± 1.4
	(11.2 - 18.1; n=32)	(9.8 - 15.3; n=8)	(n=127)
Ear Width (mm)	10.2 ± 1.1	10.3 ± 1.6	17.6 ± 1.4
	(7.2 - 12.7; n=32)	(7.7 - 12.1; n=8)	(n=127)
Body mass (g)	60.1 ± 9.6	55.5 ± 10.4	72.6 ± 13.8
	(41.0 - 78.5; n=35)	(41.5 - 73.6; n=8)	(52.9 - 105.6; n=?)

Notes on reproductive character

Of the 24 sexually mature female lemurs in Sainte Luce, three were deemed pregnant, showing obvious signs of abdominal swelling and weighing above 70g. All three showed enlarged nipples and one was observed lactating. Two were captured in September and the third in November. A further individual, captured in late August, expressed menstrual blood, indicating that she was sexually mature at this time. Two infants observed together in October (likely a sibling pair given their similar developmental stage, offering evidence for a litter size of two neonates) also points to conception in late August, if gestation time is analogous with *M. murinus*. Conversely none of the seven sexually mature female individuals captured at Nahampoana showed any sign of pregnancy, although one large female (73.6g) showed signs of having recently nursed and may have given birth very late in the season. A further documented observation of a very young juvenile in Sainte Luce in January provides some evidence for the capacity of females to produce two litters per year. The sample size of sexually mature males across both localities was small (n=12), with testicular volume only calculated for ten individuals. Maximal testicular volume (2.32ml) was recorded in August. The lowest recorded value (0.23ml) was obtained from a fully mature adult individual in June (Nahampoana), a period in which no sexual activity was expected.

Table 13a.

Biometric characteristics for a selection of eastern *Microcebus* species. Figure adapted from Rasoloarison et al, 2013 with values for *M. tanosi* updated to include data collected in this study. Note that other species are represented by a limited number of individuals. Species are displayed from the northernmost species *M. mittermeieri* (left) to the southernmost species *M. tanosi* (right).

Trait	*M. mittermeieri* (Marojejy)	*M. simmonsi* (Tampolo & Ste Marie)	*M. lehilahytara* (Ambohitantely)	*M. marohita* (Marolambo)	*M. rufus* (Andrambovato)	*M. tanosi* (All localities)
Total length (mm)	263.2 ± 12.28 (256.0 - 285.0; n=5)	279.0 ± 10.21 (263.0 - 295.0; n=12)	223.0 ± 6.00 (228.0 - 240.0; n=4	280.5 ± 7.78 (275.0 - 286; n=2)	231.6 ± 8.44 (220.0 - 241.0; n=5)	255.0 ± 11.4 (214.0 - 298.0; n=91)
Tail length (mm)	145.0 ± 9.33 (137.0 - 160; n=5)	139.8 ± 6.52 (128.0 - 148.0; n=12)	119.7 ± 7.41 112.0 - 129.0; n=4)	139.0 ± 8.49 (133.0 - 145.0; n=2)	119.4 ± 3.29 (115.0 - 124.0; n=5)	132.7 ± 9.0 (91.0 - 105.0; n=91)
Head-body length (mm)	118.6 ± 4.16 (115.0 - 125.0; n=5)	131.8 ± 6.27 (123.0.0 - 141.0; n=12)	111.5 ± 3.00 (110.0 - 116.0; n=4)	135.3 ± 4.16 (132.0 - 140.0; n=3)	108.6 ± 7.47 (100.0 - 118.0; n=5)	121.7 ± 5.5 (109.0 - 153.7; n=91)
Hind foot length (mm)	33.2 ± 0.84 (32.0-34.0; n=5)	34.2 ± 1.03 (33.0 - 36.0; n=12)	30.0 ± 0.57 (30.0 - 31.0; n=4)	34.7 ± 0.58 (34.0 - 35.0; n=3)	31.6 ± 0.64 (31.0 - 32.0; n=5)	27.5 ± 4.2 (15.0 - 33.0; n=74)
Ear Length (mm)	18.4 ± 0.55 18.0 - 19.0; n=5)	19.2 ± 0.83 (18.0 - 20.0; n=12)	19.8 ± 1.70 (18.0 - 22.0; n=4)	18.7 ± 0.58 (18.0 - 19.0; n=3)	19.0 ± 0.22 (19.0 - 19.5; n=5)	16.2 ± 2.7 (9.8 - 19.1; n=88)
Body mass (g)	56.4 ± 3.85 (50.0 - 60.0; n=5)	60.6 ± 6.50 (51.0 - 74.0; n=12)	39.3 ± 7.18 (35.0 - 50.0; n=4)	78.0 ± 12.77 64.0 - 89.0; n=3)	37.9 ± 4.28 (33.0 - 44.5; n=5)	54.7 ± 7.7 (35.0 - 81.0; n=91)

Table 13b.

Additional biometric comparison of eastern mouse lemur species. Figure adapted from Louis et al, 2006, again with values for *M. tanosi* updated. Species are displayed from the northernmost (left) to the southernmost species (right). *Includes juvenile individuals.

Trait	*M. mittermeieri* (Anjanaharibe-Sud SR)	*M. simmonsi** (Betampona SR)	*M. rufus* (Ranomafana NP)	*M. jollyae* (Kianjavato)	*M. tanosi* (All localities)
Total length (mm)	233.0 ± 0.4 n=5	270.0 ± 2.1 n=6	236.0 ± 1.2 n=15	251.0 ± 0.5 n=3	255.0 ± 11.4 (214.0 - 298.0; n=91)
Tail length (mm)	130.0 ± 0.2 n=5	142.0 ± 1.0 n=6	117.0 ± 0.8 n=15	122.0 ± 0.1 n=3	132.7 ± 9.0 (91.0 - 105.0; n=91)
Head-body length (mm)	120.0 ± 0.2 n=5	128.0 ± 1.2 n=6	119 ± 0.4 N=15	129.0 ± 0.4 n=3	121.7 ± 5.5 (109.0 - 153.7; n=91)
Body mass (g)	44.1 ± 7.4 n=5	64.8 ± 17.5 n=6	43.7 ± 4.2 n=15	61.3 ± 4.5 n=3	54.7 ± 7.7 (35.0 - 81.0; n=91)

Discussion

This study demonstrates that subtle morphological differences exist between isolated con-specific populations, supporting similar findings observed in both *M. murinus* and *M. griseorufus* (Heckman et al, 2006; Lahann et al, 2006). All populations are considered independent, separated by geographical distance and habitat discontinuity (see **Chapter 2**, **Species distribution**) although at present, the extent of genetic exchange between populations is unclear. Studies on *Eulemur collaris*, a coexisting species in the region, albeit with different dispersal capabilities, show some low-level genetic exchange across the landscape (Bertoncini et al, 2017; Hyde Roberts et al, 2020). However, dispersal between distant sites is considered insuperable for mouse lemurs, despite their ability to use connective habitats (Blanthorn et al, 2013). Although based on a relatively limited dataset, this study indicates that body length in individuals from Sainte Luce are significantly longer than in individuals from the other three study groups, whereas hind foot length, tail length and ear length appear to be greater in the Ivolo sub-population. Interestingly, the phenotypic trait (see **Appendix**; **Phenotypic variation**) of having a black tipped tail appears to be unique also to this group, although it is unclear whether such traits are linked. The population at Ivolo appears to be highly distinctive, with 100% of the 15 individuals measured correctly assigned to the group. Similarly, the Sainte Luce population is relatively distinct (85.7% of individuals correctly assigned), whilst individuals from Nahampoana appear to exhibit more intermediate characteristics. In contrast, individuals from the Lost Rainforest population appear to be comparatively smaller. However, variations do not appear to follow any obvious environmental gradient and instead may be the result of localised phenomena or study sample.

Overall, the bulk of inter-population variance was attributed to larger hind feet, a larger tail and larger ears, which are all most positively associated with individuals from Ivolo. It is plausible that both a longer tail and larger hind feet convey locomotive benefits and improved balance as in mice (Siegal, 1970). Similarly, enlarged extremities have been associated with thermoregulation (Allen, 1877; Webster, 1966), with mice reared at higher temperatures known to develop longer tails (Harrison, 1958). It is therefore possible that increased temperatures associated with habitat degradation (Ganzhorn and Schmid, 1998; Lehman et al, 2006; Senior et al, 2017) may be driving subtle trait divergence. Alternatively, individuals from Ivolo spend more time actively hunting invertebrate prey, favouring agility, balance and heightened auditory sensing (Rosowski, 1994). A further possibility could be that communicative calls are diverging between populations (Zimmermann and Hafen, 2001). Notably, ear length is also an important discriminatory feature of galago species (Masters and Bragg, 1999). However, testing these

hypotheses is beyond the scope of this study and there is currently no evidence for any environmental mechanism driving trait divergence. The second most notable explanatory function indicated a positive correlation between body length and the Sainte Luce population, however it is difficult to explain this result in an adaptive sense, although larger body size could infer improved thermal conservation (Randrianambinina et al, 2003; Lahann et al, 2006; Kobbe et al, 2011; Vuarin et al, 2013). The difference observed in total length between both Sainte Luce and Ivolo populations from those at Nahampoana and the Lost Rainforest, effectively separates the focal populations into two 'larger' (Sainte Luce and Ivolo) and two 'smaller' groupings (Nahampoana and Lost Rainforest).

Genetic results provide strong evidence that a single species of mouse lemur occupies the littoral forests of Sainte Luce, with sympatry unlikely. Similarly, although this study found no evidence for the coexistence of *M. tanosi* and *M. ganzhorni* at Nahampoana, the reserve is a likely contact zone, situated just 1.5km from Mandena, the type locality of *M. ganzhorni*. This finding is quite surprising given that both sites are linked by continuous but heavily modified habitat but matches other studies that have found no distributional overlap between the species (Rakotondranary et al, 2011; Hapke et al, 2013). The biometric data collected at Nahampoana, although limited (n=10), indicates that individuals here are slightly smaller on average than *M. tanosi* from Sainte Luce and intriguingly present a 'grey' phenotype, reminiscent of *M. ganzhorni* (see **Appendix**; **Phenotypic variation**). Since the data available in this study is insufficient to draw statistical comparisons between species, lacking *M. ganzhorni* data, the study cannot examine assess biometric convergence between species. The smaller average size of the animals in Nahampoana in relation to the other populations may simply be down to the proportion of sub-adults in the sample. Alternatively, it may indicate that some degree of introgression, although such cross-lineage mixing is currently unknown within the genus (U. Radespiel. pers. comm). A number of unusual phenotypes were observed within the limited number of mouse lemurs captured at Nahampoana, including individuals with markedly reduced ear size, in some cases to the extent that normal function was likely impeded. Although external traits have not been treated statistically here, *M. tanosi* and *M. ganzhorni* appear morphologically distinct, with *M. ganzhorni* exhibiting larger average body size, ear size and hind foot length (Rakotondranary et al, 2011; Lahann, 2006). Such maintained trait divergence, despite sharing homogenous habitats, supports the hypothesis that *M. ganzhorni* only recently colonised the littoral forests (Hapke et al, 2007).

Although past studies have found some subtle evidence for sexual dimorphism in *M. murinus* (Kappeler, 1990; Jenkins and Albrecht, 1991 Kappeler, 1991; Clair, 2007; Thomas et al, 2015),

this study found no evidence for similar sex-specific differences in *M. tanosi*. Whilst variation in body mass during gestation means that female weight varies more than males, no significant difference was found across six size related traits. Furthermore, no other *Microcebus* species are known to exhibit sexual dimorphism (Rasoloarison et al, 2000). As noted by Louis et al (2006), there also to be no latitudinal gradient to trait pattern amongst the eastern forms, as has been demonstrated in the west (Rasoloarison et al, 2000), where body mass decreases north to south. In the original description of the species, Rasoloarison et al (2013) concluded that *M. tanosi* is 'intermediate in all cranial and external characteristics but has a relatively long head-body length and relatively long ears for its body mass'. Indeed, the additional biometric precision afforded in this dataset supports this, at least in terms of total length and body mass. However, ear length in *M. tanosi* appears to be shorter than in other eastern species, although this may be explained by the inclusion of individuals with unusually reduced ears at Nahampoana. Hind foot length similarly appears to be shorter in *M. tanosi* than in other eastern species.

The determination of age class based on general field assessment, time of year and body mass is a useful diagnostic tool for the mouse lemurs. Examination of dental development is certainly not a practical means of determining age class in the field, with measurements often taken under challenging circumstances. A previous study comparing the morphology of *Microcebus* spp. in the southeast (Rakotondranary et al, 2010) did not capture any *M. tanosi* (referred to as *M. rufus*) between September and November and so instead inferred the minimum adult size from a study on *M. rufus* from the humid forests of Ranomafana National Park (Blanco, 2008). In this instance, the maturity threshold was set at 34g, however it is now clear that *M. rufus* and *M. tanosi* are not immediate genetic relatives (Yoder et al, 2016b; J. Poelstra. pers comm), and therefore the inferred measurements are likely erroneous to some degree. Two juvenile individuals captured in this study (weighing 34g and 36g) would have been considered as adults by Rakotondranary (2010), however both individuals, captured in December and May respectively, do not fit into the developmental schedule of supposed adulthood. As a result, the average weight of the species across its range (**Table 9**), likely represents a slight under estimation of the true value, as the dataset includes low body mass individuals from Mahamavo (<40g). Similarly, the female individual that now represents the type specimen weighed only 49g and may actually also be a sub-adult rather than a fully mature adult.

It is important to note that several caveats should be considered when evaluating the data and comparing localities and populations. The timing of the studies is a critical consideration. Mouse lemurs are known to develop extremely quickly (Glatston, 1979; Wrogemann and Zimmermann,

2001; Randrianambinina et al, 2003; Blanco et al, 2015) and although they adhere to a strict breeding season, study timing may have introduced significant variation into measurements (Atsalis, 1999b; Schmid, 1999; Blanco, 2011). Although body mass is perhaps the most reliable measure for inter-species and inter-population comparison, adults in reproductive condition or a reproductive state (i.e. pregnancy) will likely be heavier than individuals of a similar age out of breeding season. Indeed, the heaviest individual in the study was a pregnant female captured in December 2009 in the rainforest of Enato, weighing 81g. In contrast, the heaviest male in the study, captured in September 2017 in Sainte Luce weighed 72g. Given their rapid development, a period of just a few weeks between measurements could introduce notable variation, although this study did not find significant difference in body mass between populations overall. Seasonality may also be in part responsible for the smaller individuals observed at Nahampoana Reserve, which were captured in May/June and may have been out of condition. However, it does not explain the lower average body weights of individuals captured at the Lost Rainforest site.

A further important source of variation may originate from the different measurement techniques employed by individual researchers and the set of circumstances associated with each study. Measurements taken at Ivolo and the Lost Rainforest were recorded by a different research team than for those at Sainte Luce and Nahampoana, although standard definitions were followed. It is important to recognise that measurements obtained in some studies were taken on sedated (Rakotondranary et al, 2010; Hapke and Andrianjaka, unpub. 2009) and even euthanized animals (Rasoloarison et al, 2015), whilst those collected in this study and the Lost Rainforest were obtained from fully conscious animals and although great care was taken and precision was a priority, some measurements (particularly bone length approximations) may show some degree of inaccuracy. It is plausible therefore that the significant result found for femur length, varying between the populations in Sainte Luce and Nahampoana could be a type I error. Furthermore, trapping and capture techniques introduce an unavoidable source of variation into the dataset, as neither technique discriminates between seized individuals, although both methods were based on the assumption of an evenly distributed sex ratio (Radespiel et al, 2000). As a result, datasets vary in the proportion of sexes and age classes. This is a particular problem with small and limited datasets. Trapping during the colder months (April - July) also risks capturing small animals including juvenile or immature individuals born in the previous birthing period. It is possible that such individuals were included in some datasets (e.g. Rakotondranary et al, 2010).

The limited number of *M. tanosi* captured in Sherman traps in this study is striking, especially when trapping rates of other mouse lemur species across Madagascar are considered (Radespiel

et al, 2003; Weidt et al, 2004; Lutermann et al, 2010; Blanthorn et al, 2013; Blanco et al, 2015). In many instances, reported trapping success is high for *Microcebus* spp. and inferred population densities can reach as high as 360-400 individuals per km^2 (Hladik et al, 1980; Harcourt and Thornback, 1990). However, a number of other studies have reported similarly low trapping success (Atsalis, 2008; R. Rakotondravony. pers. comm; A. Yoder. pers. comm). Similarly, past attempts to capture mouse lemurs in Sainte Luce have experienced difficulties (J. Ganzhorn. pers. comm) and other projects in the eastern rainforests have resorted to direct captures due to low trap success (R. Rakotondravony – Mouse lemur workshop 28-07-19). In contrast, trapping rates in the proximal and highly homogenous littoral forests of Mandena are much higher (Lahann et al, 2006; Blanthorn et al, 2013), suggesting that it is not the underlying habitat type affecting mouse lemur abundance and capture success. Previous studies in Mandena also report trapping success to be highly seasonal, with captures ranging between 1% (February and March) to 13% (June and July) (Lahann et al, 2006; Blanthorn et al, 2013). The comparatively low capture rates found in this study (max 0.54% in September) therefore raise a number of interesting socio-ecological questions, and points to a deeply rooted behavioural separation between the species.

It is now evident that *M. tanosi* in Sainte Luce occur at lower population densities than *M. ganzhorni* in Mandena (Ganzhorn et al, 2008 and see **Chapter 6**) and lower capture rates are epiphenomenal. Since traps were set across a variety of habitat types in Sainte Luce (e.g. forest edges, secondary forest, intact forest interior), it seems unlikely that capture success is a result of trap placement. One potential explanation may be that *M. tanosi* possesses inherent behavioural traits that make it reluctant to enter traps. A further possibility is that *M. tanosi*, which can largely be considered a rainforest adapted species given its known distribution, is not particularly well adapted to the less productive littoral forest environment and therefore occurs at low density in this habitat type. However, anecdotal evidence from other sites (e.g. Tsitongambarika rainforest) suggests that *M. tanosi* is also difficult to capture and similarly exists at relatively low densities (G. Donati. pers. comm). In Sainte Luce, both trapped and directly captured mouse lemurs appear to be associated with *Instia bijuga*, *Vaccinium laevigatum, Sarcolaena multiflora*, *Pandanus dauphinensis* and *Diospyros spp.* whilst in Nahampoana, over 50% of captures were made in the introduced strawberry Guava (*Psidium cattleianum*).

The heavily skewed sex ratio observed in this study (37:12) in favour of females may also reflect behavioural traits and provide clues to the species' social organisation. Although the social organisation of most mouse lemur species remains unstudied, in several species (e.g. *M. berthae*, *M. rufus*, *M. murinus* and *M. ganzhorni*) male individuals are known to range widely during the

breeding season (Atsalis, 2000; Radespiel, 2000; Dammhahn and Kappeler, 2005; Lahann, 2008). Therefore, a sexually active male may potentially have a better chance of encountering a baited trap as they search for receptive females. Whilst young adult males disperse from their natal ranges, females of other species (e.g *M. berthae and M. ravelobensis*) demonstrate philopatric tendencies (Radepsiel et al, 2003; Dammhahn and Kappeler, 2005; Radepsiel et al, 2009), potentially resulting in a higher density of females (multiple generations) in specific areas (Lutermann et al, 2006). Thus, sex-specific behaviours may be driving the observed demographic bias, with intra-sexual competition compelling males into environments where they are at greater risk of predation (Radespiel, 2000). Despite their ability to utilise disturbed habitats, the idea that mouse lemurs are a fragment sensitive species has been reasoned in the past, due to their susceptibility to predation whilst passing through areas with inadequate foliage cover (Isebell, 1994; Goodman et al, 1993; Beier and Noss, 1998). As a result, forest fragmentation and habitat degradation may be driving a biased sex ratio in favour of females.

Compared to Sainte Luce, mouse lemur abundance at Nahampoana appears high, although the skew persists in direct capture data, with a ratio of 9:1 in favour of females. Given that most captures in this study took place within limited areas of forest, the hypothesis of increased male mortality, especially if subordinate males are chased away from their natal territory (Hardy, 2002), combined with female philopatry is plausible. Similarly, in Enato and Ivolo, A. Hapke and N. Andrianjaka captured 17 individual *M. tanosi* with a 12:5 female to male ratio in October 2009, and P. Wright captured 11 individuals with a 7:4 female to male ratio at the Lost Rainforest site in October 2016. In contrast, trapping at Mandena during the 2013 austral winter revealed an almost 50:50 sex ratio in *M. ganzhorni* (Blanthorn, 2013). Furthermore, a comprehensive study at Ranomafana National Park captured greater numbers of male *M. rufus*, but presumed an equal underlying sex ratio (Atsalis, 2008). However, this situation is further complicated by a multitude of factors affecting hibernation patterns and energy saving strategies. Whilst there is currently no evidence that *M. tanosi* undergoes periods of sustained hibernation in Sainte Luce, the large numbers observed in Nahampoana in May suggests that further work is necessary.

Despite all of the hard work that has been put in to trapping mouse lemurs and other species across Madagascar, publications rarely provide capture rates, and little detailed biometric data is available. There is now a clear need for a centralised database for trapping and morphometric data to complement published genetic sequences. This study makes clear that much useful data exists in the private datasets of individual researchers that if accessible could provide great utility. If identifiable differences in morphology and phenotype can be diagnosed reliably, such features

could provide implicit benefits for conservation. For example, Endangered species that are traded or trafficked could be more readily identifiable and traced to their origin (Nekaris and Jaffe, 2007). However, in order to properly encompass the broad and often highly subtle variation across a species range, wide geographical sampling would be required. As a result, such undertakings are not always feasible, and the ethics associated with capturing and processing large numbers of animals must be taken into account. However, morphological studies can evidently reveal broad environmental patterns and elucidate landscape scale variation (Olsen, 1979; Schimd and Kapperler, 1994; Bearder, 1999; Masters and Bragg, 2000; Rasoloarison et al, 2000; Nekaris and Jaffe, 2007). It is now clear that an integrative approach that combines refined genetic analysis, conscientious morphological assessment, sophisticated ecological experiment and broader phylogeographical sampling is essential in obtaining a true understanding of how a species interacts with its environment.

Whilst major phylogeographical effects clearly impact population substructure of *Microcebus* species (Pastorini et al, 2003; Mayor et al, 2004; Louis et al, 2006), additional factors such as forest fragmentation, population bottlenecks and stochastic events continually modulate these general patterns. This study found no obvious environmental gradient driving trait divergence, indicating that localised effects may be responsible for the subtle intra-specific differences between isolated populations. Disentangling the causal mechanisms that influence the trajectory of trait divergence therefore requires a deep understanding of a species' ecology and local environment, as complex factors such as habitat structure, resource availability, predator-prey dynamics and competition interact (Schäffler et al, 2015). In summary, this study presents a full biometric characterisation of *M. tanosi* across its known range, compiles all available biometric and phenotypic data and re-assesses published literature in line with the modern understanding of the species' distribution. The identities of all animals captured at both Sainte Luce and Nahampoana are confirmed genetically. The study concludes that there is no evidence for sexual dimorphism in *M. tanosi* based on external biometric character and provides a new framework for assessing age class. This chapter also presents the first information pertaining to the reproductive schedule of the species and provides data on trapping success and comparative capture techniques. Foremost, this study provides evidence for the existence of subtle intra-specific biometric differences between four populations with restricted gene flow, identifies pertinent traits, and provides potential evidence for cross lineage hybridisation between two proximal species based on phenotype. The study emphasises the utility of *Microcebus* as a model genus for investigating the drivers behind the great patterns of biodiversity across Madagascar.

CHAPTER 4

Ranging behaviour and social system

Background

The socioecological model developed throughout the 1960s and 1970s (Darwin, 1871; Crook, 1964; Verner, 1964; Orians, 1969; Trivers, 1972), provides a robust theoretical framework for the study of animal social systems and facilitates a functional explanation for the range of mating systems observed across the natural world (Emlen and Oring, 1977). One of the fundamental tenets of the model, is that a species' social organisation, structure and mating system is to some extent predictable (Emlen and Oring, 1977; Kappeler and van Schaik, 2002). Based on a limited number of environmental variables, in mammals and birds at least, the higher the potential for multiple mate monopolization, the greater the potential expression of sexual selection and tendency towards polygamy. Whilst the distribution of animals of both sexes can be expected to align with that of important resources, modulated by predator relationships (Clutton-Brock and Harvey, 1977; 1978), an important distinction is drawn between males and females in the wild. Whilst females primarily organise their spatial distribution in accordance with resources such as food and shelter (Jarman, 1974; Sterck et al, 1997), males are also driven to engage in intra-sexual competition for access to fertile females (Clutton-Brock, 1989). These inter-sexual differences, linked to fitness, have a profound influence on the expression of behaviour, physiology and morphology (Clutton-Brock and Parker, 1992; 1995). As females may only be receptive or fertile for a limited period of time, they may be regarded as an additional resource for which males compete (Trivers, 1972; Emlen and Oring, 1977). As a consequence, the degree to which specific behavioural and physical traits are manifest between the sexes can provide important indicators that help diagnose a species' social organisation and structure (Kappeler and van Schaik, 2002).

Primates have long been known to display a broad and diverse range of social behaviours and mating strategies (Crook and Gartlan, 1966; Eisenberg et al, 1972; Clutton-Brock, 1974; 1989; Clutton-Brock, 1977; Kappeler and van Schaik, 2002; Dunbar, 2013) and their study has played an important role in developing our understanding of how underlying ecological factors underpin and govern these systems. Based on the broad stability of the theoretical model, decades of field studies have now demonstrated that a great degree of social complexity exists within the order,

and as a result, many deeper questions have arisen. Given our emergent understanding of the hidden diversity within the nocturnal primates, and the rapid increase in the number of recognised species (Bearder et al, 1995; Groves, 2000; Rasoloarison et al, 2000; Louis et al, 2006; Nekaris and Jaffe, 2007; Rasoloarison et al, 2013; Hotaling et al, 2017), it is now evident that the full range and diversity of social adaptations in terms of organisation, structure and mating systems is not yet fully understood. As a consequence, clear patterns in the expression and manifestation of different social systems, and how these relate to ecological conditions and phylogenetic factors is not yet fully discernible. In this chapter, the term 'social organization' is used to refer to the size, sexual composition and spatio-temporal cohesion of a society and 'social structure' refers to the expressed pattern of social interactions and resulting relationships among all members of the society (Kappeler and van Schaik, 2002). The definition of mating systems follows Clutton-Brock, 1989 and Kappeler and van Schaik, 2002.

Whilst the manifestation of subtly different social systems appears fundamentally dependent on territoriality and the reproductive synchronicity of females (Altmann, 1990; Mitani et al, 1996; Dunbar, 2000; Kappeler, 2000; Eberle and Kappeler, 2002), variation in social system exists even amongst closely related genera (e.g. within the Cheirogaleidae), and even between sympatric species within the same family (*Cheirogaleus medius* and *Mirza coquereli*) (Kappeler, 1997b; Bearder, 1999). A substantial body of literature now exists, detailing the social lives of a wide range of nocturnal primates (e.g. Bearder and Doyle, 1974; Sterling, 1993; Kappeler, 1997; Atsalis, 2000; Gursky, 2000; Schülke, 2005; Nekaris, 2006; Biebouw, 2009), and it is apparent that each species is remarkable and different in its own right. Resource availability is known to be a key predictor of ranging behaviour in primates (Curtis and Zaramody, 1998; Wallace, 2006; Boyle et al, 2009; Donati et al, 2011; Schwitzer et al, 2011; Campera et al, 2014), therefore some degree of variation in expressed social organisation and social structure may be expected between habitat types and across ecological gradients, at species level. Furthermore, a wide range of additional ecological variables, often site-specific (e.g. habitat structure, predator interactions, population density, dispersal strategy) (Clutton-Brock, 1975; 1977b; Goodman et al, 1993, Irwin, 2008), interact and further modulate the expression of social behaviours (Atsalis, 2008). Similarly, phylogenetic factors and the plasticity of social behaviour amongst closely related, con-generic species with shared life history traits require further exploration.

Mouse lemurs (Genus *Microcebus*) have long been regarded as ideal model taxa to study social organisation and mating systems in primates and are now amongst the most broadly researched nocturnal primate groups (e.g. Fietz, 1999; Radespiel, 2000; Atsalis, 2000; Schwab, 2000;

Dammhahn and Kappeler, 2005; Génin, 2010). The genus is characterised by remarkable species richness and a wide range of inter-species spatial interactions (Yoder et al, 2016b). Mouse lemur species are widely distributed and abundant throughout Madagascar's forested habitats, occupying a diverse range of ecological settings (Eberle and Kappeler, 2002; Mittermeier et al, 2010). Furthermore, as small bodied, omnivorous species (Hladik et al, 1980; Mittermeier et al, 2010), they are perhaps less susceptible to resource patchiness than other larger species with more specialised diets (Kappeler and van Schaik, 2002). Although individual mouse lemurs do not exhibit any synchronicity when foraging (Charles-Dominique, 1978; Eberle and Kappeler, 2002), it is clear that like other nocturnal solitary foragers, they exist within complex social communities (e.g. Martin, 1972b; Clark, 1985; Bearder, 1987; Kappeler, 1997; Gursky, 2000; Müller and Thalmann, 2000) and continually engage in complex social interactions (Zimmermann, 1995; Schmid, 1998; Braune et al, 2005; Dammhahn and Kappeler, 2005; Génin, 2010). Mouse lemurs are also strict seasonal breeders, with sexual interactions restricted to the austral summer months (Petter-Rousseaux, 1968; Martin, 1972b; Atsalis, 2008; Blanco, 2008; 2011). Females exhibit pronounced reproductive synchronicity, and as a result, the potential for individual males to monopolise receptive females is limited. As a consequence, sexually mature male individuals should in theory roam more widely during the breeding season in order to increase their encounter rates with fertile females (Emlen and Oring, 1977; Ims, 1988; Schwagmeyer, 1988; Dunbar, 2000.

Indeed, much effort has been focused on the study of mating systems in wild mouse lemur populations over the past five decades, and on the extent of intra-sexual competition between males and the degree to which dominant individuals can monopolise females (Petter, 1962; Martin, 1972b; Barre et al, 1988; Pages-Feuillade, 1988; Radespiel, 2000). As both fieldwork and captive research has developed and additional species have been studied, a generalised pattern has materialized. All wild populations studied so far appear to exist within dispersed multi-male, multi-female communities with overlapping home ranges, exhibit promiscuous mating systems, and show no clear evidence for the monopolisation of females by dominant males (Atsalis, 2000; Radespiel, 2000; Weidt et al, 2004; Dammhahn and Kappeler, 2005; Lahann, 2008; Hending et al, 2017). Such characteristics are hallmarks of a pronounced 'scramble' competition mating system (Wells, 1977; Schwagmeyer, 1988; Clutton-Brock, 1989; Tew and MacDonald, 1994; Kappeler, 1997b; Kappeler and van Schaik, 2002). Instead, male-male competition manifests through high reproductive capacity (Harcourt et al, 1981), sperm competition (Eberle et al, 2007) and possibly enhanced searching and cognitive ability related to locating estrous females (Radepsiel, 2000). Male mouse lemurs are well known to greatly increase reproductive capacity during the breeding season, exhibiting amongst the largest relative testicular size of any primates

(Harcourt et al, 1981; Fietz, 1999; Schwab, 2000; Rode-Margono et al, 2015). Such capacity is often pronounced in species where females typically mate with multiple male partners (Kappeler and van Schaik, 2002). Similarly, the absence of clear sexual dimorphism in any studied species (Mittermeier et al, 2010; **Chapter 3**; but see Kappeler, 1990; Clair, 2007; Thomas et al, 2015), particularly within traits indicative of intra-sexual competition (e.g. body size and canine size), further suggests that direct male competition is displaced (Kappeler and van Schaik, 2002).

In contrast however, captive studies have found subtle evidence for intra-sexual competition, with paternity studies revealing that a small number of individuals sire the majority of offspring, and furthermore, these individuals are associated with larger body sizes and more pronounced sexual characteristics (e.g. enlarged testicular size) (Perret et al, 2001; Andrès and Silignac, 2003). In addition, dominant male individuals were able to supress rival reproductive activity by means of urinary pheromones (Perret, 1992). However, a further study found no correlation between dominance and the number of offspring sired (Radespiel et al, 2002). The seemingly conflicting evidence obtained from studies conducted both in the wild and in captivity serve to underline the complex nature and malleability of social structures under different environmental conditions. The constraints of captive studies evidently distort the underlying ecological fabric on which social systems are based and result in differentiated social manifestations, however, it is apparent that controlled experiments can reveal important insights into the nature of social behaviours.

It is further important to recognise that female individuals are not merely inert in the mating process and similarly adopt strategies to maximise their reproductive investments. Given that female mouse lemurs are both socially dominant (Kappeler, 1996; Radespiel and Zimmermann, 2001), and exclusively responsible for infant rearing (Eberle and Kappeler, 2006), mate selection is an important consideration (Kappeler and van Schaik, 2002). Whilst females of other primate species adjust their spatial distribution, or degree of reproductive synchrony (Zinner et al, 1994) the strategies of female mouse lemurs in the wild remain poorly understood. However, female strategies are known to centre around stable matriarchical structures (Radespiel et al, 2001; 2003; Kappeler et al, 2002; Wimmer et al, 2002; Fredsted et al, 2005) and individuals have been shown to respond positively to males who are able to produce high frequency advertisement calls for long durations (Craul et al, 2004). In captivity, females also respond less aggressively to dominant males (Perret et al, 2001). Such observations indicate that females exhibit some degree of mate choice, however the impact of such strategies within mouse lemur societies requires further study. Given that mouse lemur communities often exist at high densities (Ganzhorn et al, 2008; Mittermeier et al, 2010; Malone et al, 2013; Schäffler and Kappeler, 2013; Steffens et al, 2016)

and communicate using a variety of complex systems (Perret, 1992; Radespiel, 2000; Braune et al, 2005), affiliative social encounters and partner preferences are considered likely (Radespiel, 2000; Perret et al, 2001).

Despite being one of the most intensely researched nocturnal primate groups, at the outset of this study, only eight of the 26 recognised mouse lemur species had been well studied with regards to their home range and social organisation (Radespiel, 2000; Weidt et al, 2004; Dammhahn and Kappeler, 2005; Radespiel, 2006; Lahann, 2008; Génin, 2010; Hending et al, 2017). Although the majority of species lack study, the available data suggests that home range size not only differs markedly between species, but also that the ranging strategies adopted by each sex varies between species. Whilst the data emphasises a commonality in some aspects of social organisation, for example all species appear to exhibit substantial range overlap between sexes, the data highlights a striking discontinuity in expressed reproductive strategy. Whilst a number of studies have found the home range size of both sexes to be similar, at least during certain times of the year (*M. lehilahytsara*, *M. ravelobensis* and *M. sambiranensis*) (Randrianambinina, 2001; Weidt et al, 2004; Jürges et al, 2012; Hending et al, 2017), others have shown that male ranges are significantly larger than those of females (*M. berthae* or *M. myoxinus* and *M. rufus*) (Atsalis, 2000; Schwab, 2000; Schwab and Ganzhorn, 2004; Dammhahn and Kappeler, 2005), in some cases increasing in size during the reproductive season (*M. ganzhorni* and *M. murinus*) (Pages-Feuillade, 1988; Radespiel, 2000; Lahann, 2008). Conversely, female *M. griseorufus* appear to occupy larger home ranges than males (Génin, 2010). These variations serve to highlight the malleability within the social organisation of mouse lemurs under different ecological conditions (Schmid and Kappeler, 1998). However, given the strict reproductive seasonality of *Microcebus* spp., comparisons between studies and species are complicated by methodological differences, and disentangling genuine ecological patterns from methodological design limits the robustness of genus level conclusions.

Understanding ranging behaviour and the extent of overlap between both individuals and sexes can reveal the social organisation, social structure and mating system of a species. Combined with an understanding of sleeping group arrangement and social genetic structure (Bearder, 1987; Kappeler, 1997; Müller and Thalmann, 2000; Kappeler et al, 2002; Radespiel et al, 2001b; 2003; Wimmer et al, 2002; Fredsted et al, 2005), ranging patterns reveal the fundamental social nature of a species. At a deeper level, the ranging behaviour of both sexes provide insight into how underlying ecological factors such as resource distribution and predator avoidance influence social behaviours. However, studying and detailing the sociality of small, cryptic and highly

mobile nocturnal primate presents a substantial challenge and requires notoriously difficult fieldwork, particularly in humid eastern forests. Based on telemetric data, this study investigates the social organisation and structure of *M. tanosi* in a natural setting. Beyond providing species-specific data, this study aims to increase our broader understanding of the expression of social behaviour and explores species-level patterns within the genus *Microcebus*. The following research questions will be addressed:

1) Are there significant differences in ranging patterns between sexes and what can be inferred about the reproductive strategy of the species?
2) Do the sexes utilise their home ranges differently during the reproductive period?
3) To what extent do individual home ranges overlap and what insight does this offer in terms of understanding the social structure of the species?
4) Do environment conditions or phylogenetic relationships determine the ranging parameters of mouse lemur species?

Based on the available literature, I offer the following hypotheses:

1) Ranging patterns between sexes will show marked differences, with males ranges greater than those of females, in order to maximise encounters with potential mates. *M. tanosi* will conform to a 'scramble contest' reproductive system.
2) In order to maximise mating opportunities, male individuals will utilise sleeping sites closer to the edges of their home ranges, whilst females will prioritise security and select sleeping sites closer to their established home range centres.
3) Similar to other mouse lemur species, *M. tanosi* in the littoral forests will exhibit substantial inter-individual range overlap, with populations comprising of multi-male, multi-female social neighbourhoods.
4) Environmental conditions impart a more powerful influence on ranging behaviour than innate phylogenetic traits. As a result, the expressed ranging behaviour of *M. tanosi* will more closely resemble that of *M. ganzhorni* in the nearby littoral forests of Mandena, than those of more closely related species (e.g. *M. rufus* in the eastern humid rainforests).

Methodology

This study was conducted in the littoral forests of Sainte Luce, in the extreme southeast of Madagascar and focused on *Microcebus tanosi*, a small, arboreal and highly agile species with a mean body mass of 60g (± SD 9.6g). Population density in Sainte Luce is comparatively low relative to some other well studied mouse lemur species at ca. 0.2–3.2 ind/ha (Ganzhorn et al, 2008 but see **Chapter 6**). All focal individuals were captured and studied in a single forest fragment; S9 (**Fig. 19**) (see **Chapter 2**, **Study area**). Although a small number of animals were also studied in S8, the limited number of captures, the logistical challenges associated with the fragment and a series of collar escapes precluded comparative study. Forest fragment S9 (referred to locally as Agnalan'ambandriky) covers an estimated 346ha, with the core (215ha) classified as an IUCN category IV protected forest. The fragment is considered relatively intact compared to other remaining fragments in the region (Lowry and Faber-Langdoen, 1991; Ganzhorn et al, 2008; Temple et al, 2012), however sections in both the north and the south are degraded as a result of community resource extraction. All animals in this study were captured by means of either Sherman trapping or by direct capture techniques (see **Chapter 2**, **Trapping and capture methodology**). Captures deliberately took place within a limited patch of forest, in an attempt to target animals with overlapping or proximal ranges. Captured mouse lemurs (n=23) were fitted with lightweight (~3g) HOLOHIL PD-2C transmitters (see **Chapter 2**, **Radio-collaring)**, with battery life extended with modifications to the transmitted pulse frequency. All collars were custom fit to the individual lemur and all animals were returned to within 10m of their capture site. All study animals were considered to be adult (Groves and Harding, 2003).

Home range data was collected over two periods, between 15/08/2017 to 31/01/2018 and 21/08/2018 and 08/11/2018. Both periods coincide with the end of the austral winter and the start of the austral summer, the known reproductive phase of the species (see **Chapter 3**). Home range data consisted of a combination of nocturnal follows, sleeping site locations (detailed in **Chapter 5**) and the initial capture site. A total of 35 nocturnal follows (Altmann, 1974) were conducted by SHR throughout the study period. No individuals were studied across both periods. Nocturnal follows invariably started at dusk, circa 6pm (adjusted as photoperiod increased as the season progressed), with focal animals located at their sleep site prior to the follow. Focal animals were followed for a minimum of three hours, and a maximum of six hours, with weather conditions, follow success and practical constraints governing follow duration. Given that nocturnal follows did not extend to the entire active period of the species (i.e. dusk until dawn), nightly travel distances could not be reliably estimated or compared between sexes or individuals. Animals were

tracked using an AOR AR 8200 wide range receiver and Lintec flexible 3-element yagi antenna (148.000-151.999MHz) (BioTrack Ltd, UK). The primary headlamp used was a high powered LEDLenser H14R.2. GPS waypoints were recorded using a Garmin GPSmap62s handheld device each time a visual fix on the focal individual was attained. A discontinuous data collection regime was followed (Harris et al, 1990), whereby if visual contact was maintained, a new waypoint was registered with each significant movement or activity (e.g. feeding event, movement of >5m). If an individual was observed resting for extended periods, a single GPS waypoint was recorded. Standard 'continuous' or 'time interval' recording was attempted initially, but soon deemed an inappropriate method as the focal individual was frequently out of sight from the observer, and its locality could not be accurately determined, especially if the animal was high in the canopy, or concealed in dense vegetation (Harris et al, 1990). The average time interval between GPS fixes over the study period was 8.3minutes (minimum average = 3.4mins; maximum average = 30.0mins per follow session).

Home range analysis was conducted using software Ranges 9 v2.01 (Anatrack Ltd) (Kenward et al, 2014). Minimum convex polygons (MCPs) (White and Garrot, 1990; Powell, 2000; Campera et al, 2014) were developed using all available locational data. 100% cores with re-calculated arithmetic mean centre (rAc) peel centres were constructed. Utilisation plots depicting the area of estimated home range cores at 5% intervals from 20-100% were created and examination provided a method to determine the percentage of locations that sufficiently define a core range (Ford and Krumme, 1979), excluding probable outliers. MCP's are sensitive to peripheral waypoints (outliers) and as a result can overestimate range size (Powell, 2000). In instances where outliers greatly influenced home range estimates, lower core % thresholds were examined and adopted in order to better reflect core home range areas, excluding what are likely distant excursions (Harris, 1990; Radespiel, 2000; Kenward et al, 2014). Additional 95% and 50% fixed kernels (FK) were constructed for comparison and cross validation (Harris et al, 1990), with contours fitted to location density and with a fixed smoothing multiplier of 1. FK estimates are considered more robust than MCP's and less affected by outliers (Harris et al, 1990). Furthermore, they are constructed on the assumption that each GPS point is independent and time sequence is irrelevant (Powell, 2000).

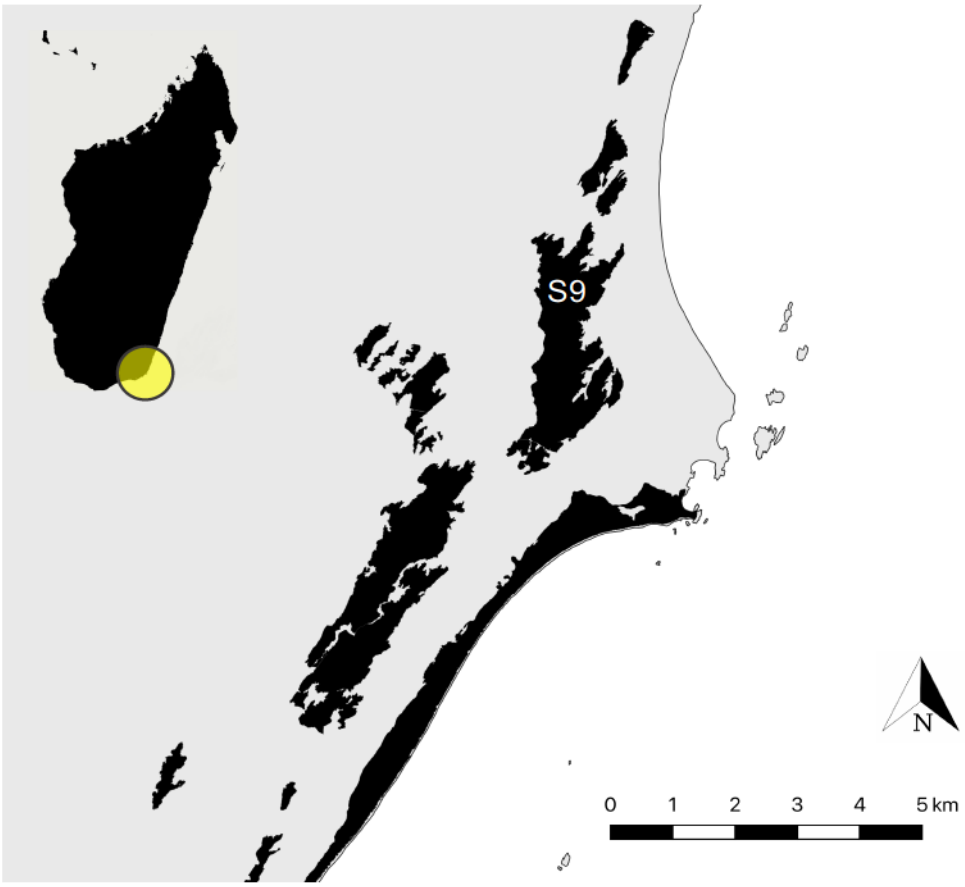

Figure 19 – Study site location (S9) relative to Madagascar and the surrounding littoral forest fragments.

Incremental Area Analysis (IAA) was performed for both model types (100% MCP, and 95% FK) in order to determine whether ranges show evidence of reaching asymptote (Harris et al, 1990, Campera et al, 2014). In cases where asymptote was not reached, subsequent statistical comparisons were conducted using linear correlation residuals. Autocorrelation of data was not considered to be critical factor in this study, since the time interval between fixes was relatively large and focal individuals were never followed on consecutive nights. Furthermore, kernel analysis is considered robust to autocorrelation effects (Harris et al, 1990; Fleming et al, 2015). GIS tools (QGIS 3.10 and Google Earth Pro 7.3.3) were used to adapt final home range estimates, where ranges overlapped unsuitable habitats (e.g. non-forest habitats) to improve the accuracy of final home range estimates. Spatial overlap of ranges was determined using GIS tools (QGIS vector analysis) and based on both MCP and FK ranges following Radespiel (2000). An overlap of 10% or greater between any two individuals indicates spatial access to one another. The distance of sleeping sites from both the estimated home range centre and boundary were calculated using GIS tools. Statistical analysis was conducted using IBM SPSS version 26

(Chicago, IL, U.S.A) with the level of significance set at p=<0.05. The relationship between the number of GPS fixes per individual and the size of the estimated home range was determined using the bivariate Pearson correlation. In cases where correlation was confirmed, between sexes comparison was tested based on residual values obtained from linear regression analysis.

Results

A total of 13 individuals (eight females and five females) were tracked sufficiently to enable home range estimation based on both resting location and ranging behaviour (a minimum threshold of ten hours nocturnal follow). Home range size differed significantly between sexes for both MCP range estimators (100% MCP's and variable core MCP's) whilst there was a strong tendency for differentiation in the 95% FK analysis, with males exhibiting a larger ranging area than females in each case (**Table 14**). Conversely, 50% FK analysis found no significant difference in the size of the core home range areas between the sexes. The median home range of female individuals was 1.4ha using both the adjusted MCP (min=0.9/max=4.6ha) and 95% fixed kernel (min=0.4/max=4.1ha) estimators. In contrast, the median ranging area of male individuals was 6.1ha (min=2.5/max=7.8ha) using the adjusted MCP method, and 4.8ha (min=1.4/max=10.5ha) using the 95% fixed kernel analysis. However, IAA revealed that not all individual home ranges reached asymptote (n males=3, n females=4). Bivariate Pearson correlation analysis revealed a significant relationship between the number of GPS fixes and the estimated 50% FK range size (r=0.621, p=0.023, n=13), the 95% FK range size (r=0.575, n=13, p=0.040), the 100% MCP (r=0.556, p=0.049, n=13) and a trend towards significance between the number of GPS fixes and variable core MCP range size (r=0.512, n=13, p=0.074). The relative locations and juxtaposition of individual home ranges are presented in **Figure 20**.

The ranges of twelve study individuals overlapped to varying extents (**Fig 20** + **Table 15**), indicating that *M. tanosi* exists within a social neighbourhood, as has been observed in other mouse lemur species. Overlap occurred both inter and intra-sexually. A single individual's range (an adult female – ML8) did not overlap with any of the other collared lemurs in this study, its range located ca. 200m to the north of the other study animals. The isolated female was excluded from overlap calculations. The median percentage overlap between all individuals in the study was 22.4% (min=0.2/max=75.8%), 13.7% (min=1.2/max=75.8%) between all female lemurs, 6.7% (min=0.6/max=56.8%) between male individuals and 32.6% (min=0.2/max=58.4%)

between male and female individuals under the adjusted variable core MCP analysis. In comparison, the median percentage overlap between all individuals using the 95% fixed kernel analysis was 13.0% (min=0.2/max=54.6%), 5.6% between females (min=1.3/max=48.3%), 5.4% between males (min=1.4/max=45.8%) and 24.7% between males and females (min=0.2/max=54.6%) (**Fig. 21**). In terms of the physical area of overlap, based on adjusted MCP's, median male-male overlap was 0.4ha (min=0.0/max=4.2ha), median female-female overlap was 0.21ha (min=0.0/max=1.9ha) and median male-female overlap was 0.9ha (min=0.0/max=2.7ha). The median overlap of all individuals was 0.9ha (min=0.0/max=4.24ha). Under the 95% FK method, median male-male overlap was 0.2ha (min=0.1/max=3.6ha), median female-female overlap was 0.1ha (min=0.0/max=0.5ha) and between sexes overlap was 0.5ha (min=0.0/max=2.0ha). Median overlap between all individuals using the 95% FK method was 0.3ha (min=0.0/max=3.6ha).

Table 14.

Estimated home range size for individual *M. tanosi* in Sainte Luce, with between sexes statistical comparisons (Anova and Mann-Whitney U test). Mean range size in parenthesis. All output (MCP's and FK's) adjusted to account for overlap with unsuitable habitats (e.g. non-forest areas). FK 50% provides a representation of core area size. *Indicates that a variable core value has been applied.

Lemur ID	Total GPS Fixes	IAA Asymptote	100% MCP (ha)	Adj MCP* (ha)	FK 50% (ha)	FK 95% (ha)
ML1 F	128.0	Y	2.0	2.0	0.5	1.3
ML2 F	62.0	Y	1.1	1.1	0.2	0.4
ML3 F	52.0	N	0.9	0.9	0.2	0.5
ML4 F	65.0	Y	8.3	4.6	1.1	3.9
ML5 F	58.0	Y	3.8	2.3	0.6	1.5
ML6 F	49.0	N	2.7	1.2	0.4	1.6
ML7 F	51.0	N	1.5	1.5	0.3	1.3
ML8 F	39.0	N	3.6	1.2	0.6	1.8
			(3.0)	(1.9)	(0.5)	(1.5)
ML9 M	68.0	N	5.2	2.5	0.6	1.4
ML10 M	80.0	Y	10.0	6.4	1.6	5.6
ML11 M	139.0	Y	16.5	7.8	3.8	10.5
ML12 M	56.0	N	6.3	4.7	0.8	2.6
ML13 M	62.0	N	6.1	6.1	0.8	4.8
			(8.8)	(5.5)	(1.5)	(5.0)
Between sexes comparison			F= 6.527; p=0.027 N=13	U= 39.000; p=0.003 N=13	F= 2.879; p=0.118 N=13	F= 4.757; p=0.052 N=13

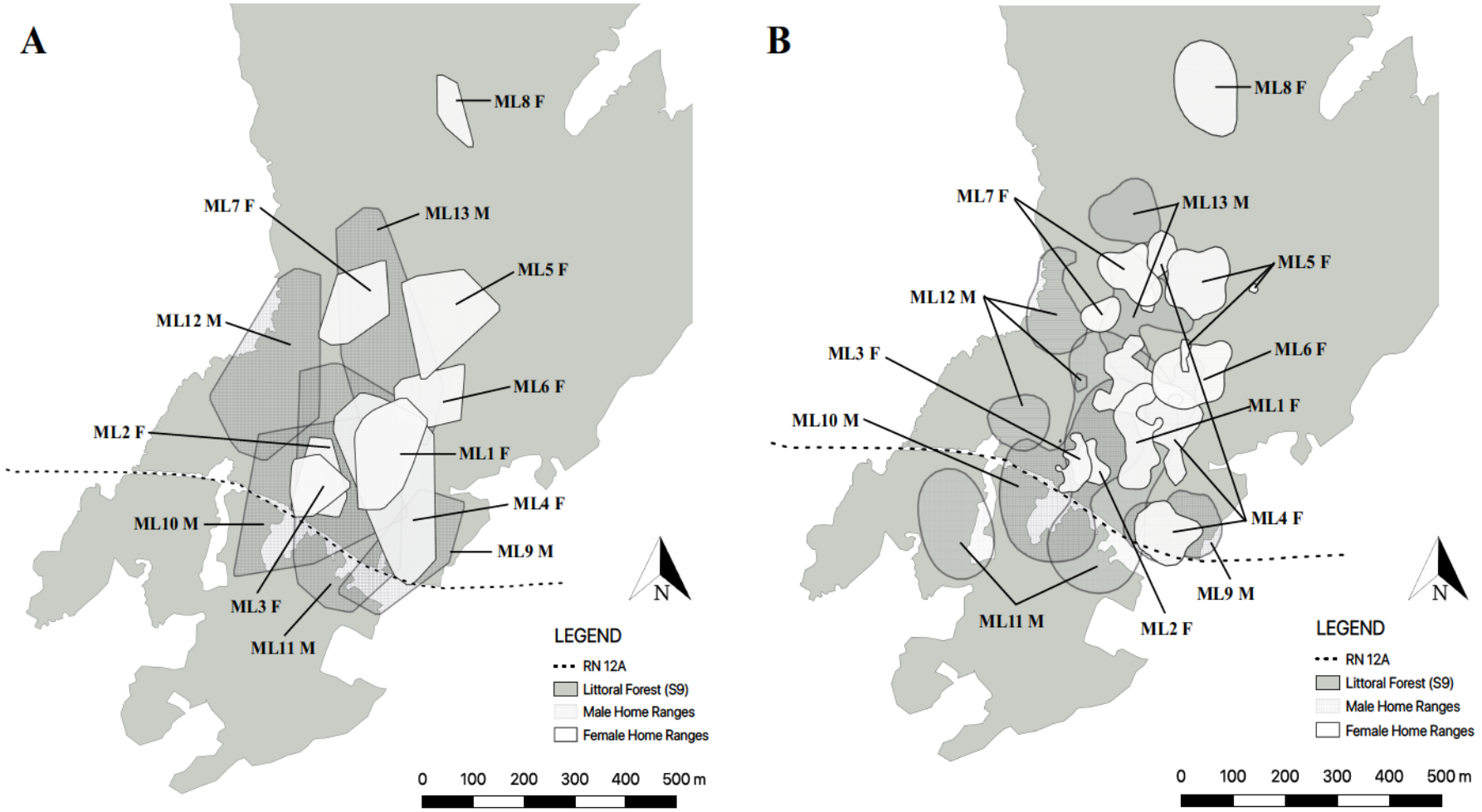

Figure 20 – The juxtaposition of all study animals home ranges', based on **A**) variable core MCP's and **B**) 95% fixed kernels. Female individuals are represented by solid colour blocks, and males (n=5) with check filled polygons. The high density of individuals supports the hypothesis of a social neighbourhood system.

Table 15.

A comparison of home range overlap between all study individuals for both the adjusted core MCP and 95% fixed kernel analysis.

Overlap matrix - Adjusted MCP's

Lemur ID	ML1 F	ML2 F	ML3 F	ML4 F	ML5 F	ML6 F	ML7 F	ML8 F	ML9 M	ML10 M	ML11 M	ML12 M	ML13 M
ML1 F (2.0ha)		X	X	67.9%	X	13.7%	X	X	X	28.6%	49.4%	X	23.7%
ML2 F (1.1ha)	X		75.8%	X	X	X	X	X	X	58.4%	55.7%	X	X
ML3 F (0.9ha)	X	75.8%		X	X	X	X	X	X	57.0%	50.4%	X	X
ML4 F (8.3ha)	67.9%	X	X		X	6.1%	X	X	36.6%	27.1%	46.2%	X	16.3%
ML5 F (3.8ha)	X	X	X	X		1.2%	X	X	X	X	X	X	14.0%
ML6 F (2.7ha)	13.7%	X	X	6.1%	1.2%		X	X	X	X	3.0%	X	6.8%
ML7 F (1.5ha)	X	X	X	X	X	X		X	X	X	X	0.2%	48.8%
ML8 F 3.6ha)	X	X	X	X	X	X	X		X	X	X	X	X
ML9 M (5.2ha)	X	X	X	36.6%	X	X	X	X		0.9%	21.2%	X	X
ML10 M (10.0ha)	28.6%	58.4%	57.0%	27.1%	X	X	X	X	0.9%		56.8%	5.3%	0.6%
ML11 M (16.5ha)	49.4%	55.7%	50.4%	46.2%	X	3.0%	X	X	21.2%	56.8%		6.7%	12.4%
ML12 M (6.3ha)	X	X	X	X	X	X	0.2%	X	X	5.3%	6.7%		X
ML13 M (6.1ha)	23.7%	X	X	16.3%	14.0%	6.8%	48.8%	X	X	0.6%	12.4%	X	

Overlap matrix - Adjusted 95% Fixed Kernals

Lemur ID	ML1 F	ML2 F	ML3 F	ML4 F	ML5 F	ML6 F	ML7 F	ML8 F	ML9 M	ML10 M	ML11 M	ML12 M	ML13 M
ML1 F (1.3ha)		X	X	24.7%	X	4.2%	X	X	X	31.2%	54.6%	X	9.9%
ML2 F (0.4ha)	X		48.3%	X	X	X	X	X	X	9.4%	52.0%	X	X
ML3 F (0.5ha)	X	48.3%		X	X	X	X	X	X	53.9%	42.1%	X	X
ML4 F (3.9ha)	24.7%	X	X		1.3%	13.5%	5.6%	X	24.0%	12.5%	32.6%	X	29.5%
ML5 F (1.5ha)	X	X	X	1.3%		4.7%	X	X	X	X	X	X	4.3%
ML6 F (1.6ha)	4.2%	X	X	13.5%	4.7%		X	X	X	X	8.7%	X	24.7%
ML7 F (1.3ha)	X	X	X	5.6%	X	X		X	X	X	0.2%	0.6%	41.1%
ML8 F 1.8ha)	X	X	X	X	X	X	X		X	X	X	X	X
ML9 M (1.4ha)	X	X	X	24.0%	X	X	X	X		X	8.5%	X	X
ML10 M (5.6ha)	31.2%	9.4%	53.9%	12.5%	X	X	X	X	X		45.8%	2.1%	1.4%
ML11 M (10.5ha)	54.6%	52.0%	42.1%	32.6%	X	8.7%	0.2%	X	8.5%	45.8%		2.3%	16.5%
ML12 M (2.6ha)	X	X	X	X	X	X	0.6%	X	X	2.1%	2.3%		X
ML13 M (4.8ha)	9.9%	X	X	29.5%	4.3%	24.7%	41.1%	X	X	1.4%	16.5%	X	

There was no significant difference in the overlap between sexes for either MCP or FK method, or between groups (male-male overlap, female-female overlap and male-female overlap) both in terms of percentage overlap and area. The maximum number of individual study females whose home ranges intersect was three, as was the case for the males, however the ranges of three individual males overlap at three localities in this study, but at just one locality between females. Standard deviations for the overlap of home ranges are high, however it is evident that most individuals, belonging to both sex classes, have spatial access to multiple potential partners (i.e. they share >10% overlap) (**Table 15** and **Fig. 22**). Male individuals had access to a median of 4 study females (min=0/max=4), whilst females had access to a median of 2 study males (min=0/max=4) based on adj. MCP home range estimates. Based on 95% fixed kernel analysis, study males had access to an average of 3 study females (min=0/max=4), with females having access to 1 study male (min=0/max=4). However, the incomplete sampling of the community means that these values can only represent minimum estimates. The largest observed shared range between two female individuals was 75.8%, whilst the maximum degree of overlap between two male individuals was 56.8% (both produced from home ranges estimated using the adjusted MCP method). In terms of area, maximum male-male shared range was 4.24ha (adj. MCP) or 3.60ha (95% FK), compared to 1.92ha (adj. MCP) or 0.55ha (95% FK) between females. Maximal male-female shared range was 2.74ha (adj. MCP) or 2.00ha (95% FK).

From values extracted from the adjusted MCP's, a significant difference was detected in the distance between sleeping sites and the home range centre point between sexes (Mann-Whitney; U=3128.000, p=0.000, N=132), with male individuals (Mdn=117.5m, min=17/max=358m) sleeping further from the calculated centre point than females (Mdn=53.76m, min=3/max=120m). Similarly, a significant difference was observed at the level of the individual (Kruskal-Wallis; H=63.842, p=0.000, N=132). There was no significant difference detected between the sexes in relation to the position of sleeping sites and the outer edge of their estimated home ranges. In contrast, in home range estimates generated by the 95% FK method, the reverse situation was found. No significant difference was detected between sexes with regard to the distance between sleeping sites and the home range centre point, but a significant difference was found between the sleeping site – range edge distance (Mann-Whitney; U=1667.000, p=0.003, N=105), with females on average nearer to the home range boundary (male Mdn=36.1m, min=1/max=65m; female Mdn=22.0m, min=0/max=60m).

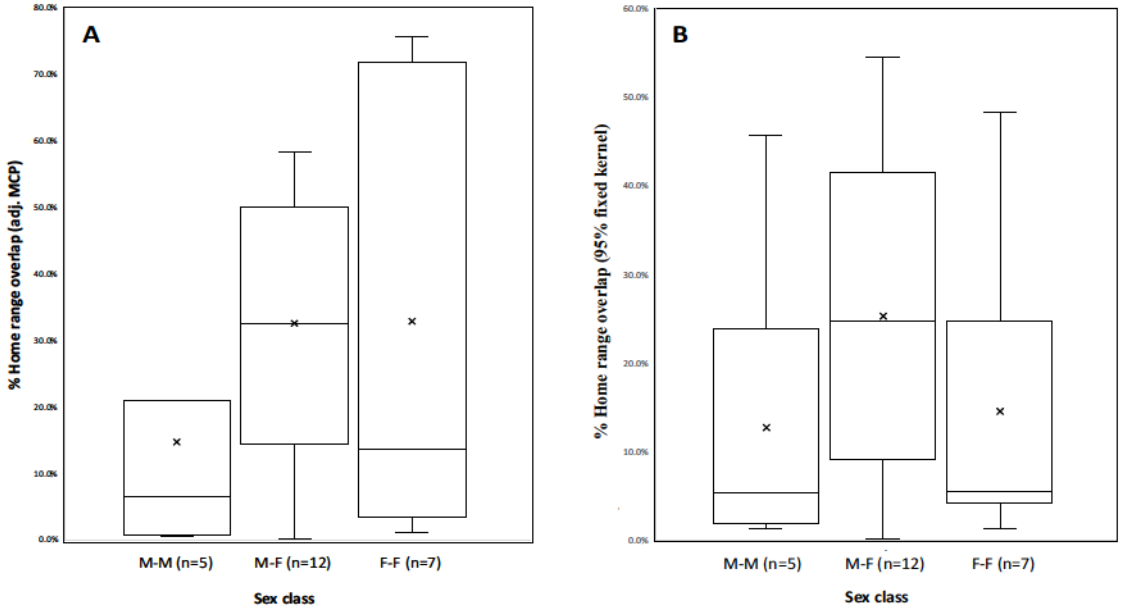

Figure 21 – Boxplots showing the percentage home range overlap of study animals for each sex class using **A**) Adjusted MCP analysis and **B**) 95% Fixed kernel analysis. 'x' represents the mean overlap percentage; the median is provided by a horizontal line and whiskers represent minimum and maximum values.

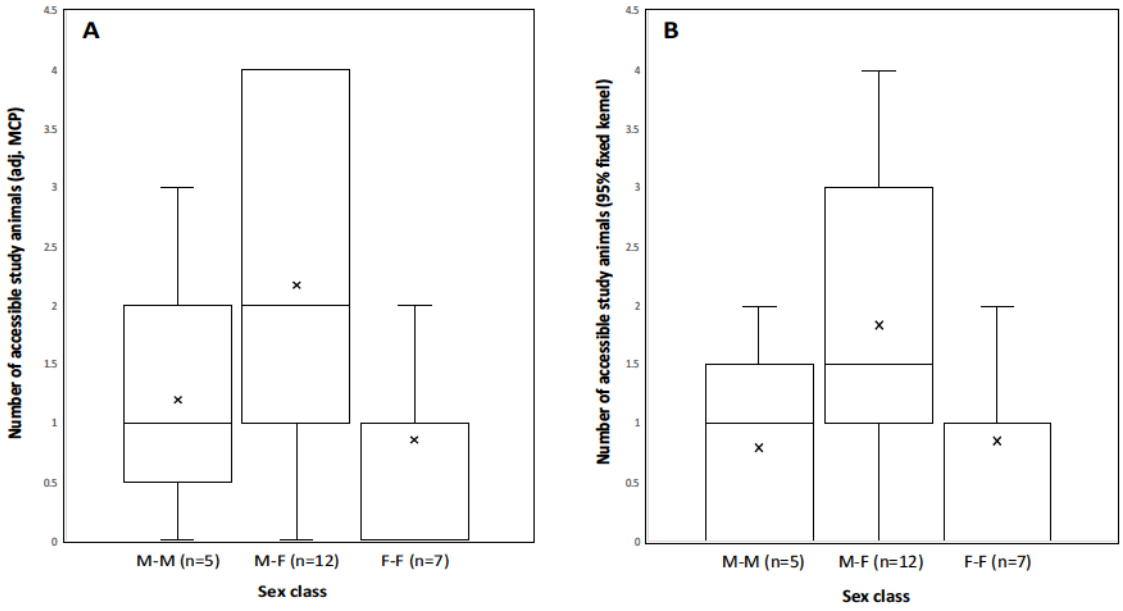

Figure 22 – Boxplots showing the number of accessible study animals available to each sex class based on **A**) Adjusted MCP home range estimates and **B)** 95% Fixed kernel home range estimates. Access assumed between individuals based on a minimum 10% home range overlap. 'x' represents the mean overlap percentage; the median is provided by a horizontal line and whiskers represent minimum and maximum values.

Discussion

Microcebus tanosi home ranges overlap substantially both inter and intra-sexually and are consistent with a dispersed social neighbourhood model of sociality and a promiscuous mating system (Jolly, 1966; Clutton-Brock, 1989; Radespiel, 2000; Hending et al, 2017). This polygynandrous modality, where social structure consists of multimale-multifemale communities with each individual having access to multiple potential mates (Clutton-Brock, 1989; Eberle and Kappeler, 2004) has so far been observed in all other *Microcebus* species studied to date (e.g. Atsalis, 2000; Radespiel, 2000; Weidt et al, 2004; Génin, 2008; Hending et al, 2017). Indeed, this social structure has been proposed as an ancestral primate social model, given its ubiquity amongst nocturnal strepsirrhines (Muller and Thalmann, 2000), although it does not accord with many 'solitary' nocturnal prosimians (Charles-Dominique, 1978; Bearder, 1987). This study provides further evidence for 'scramble' competition being the predominant explanation for male ranging patterns in wild mouse lemur populations (Harcourt et al, 1981; Clutton-Brock, 1989; Radespiel, 2000; Radespiel et al, 2001b; 2003) and finds no evidence for the monopolization of females by males. Whilst there is a substantive body of literature in support of 'contest' competition in captive settings (Trivers, 1972; Perret, 1992; Perret et al, 2001), under natural conditions most mouse lemur populations appear to tilt towards a multimale – multifemale promiscuous mating system, with overlapping home ranges and where male competition is manifested through increased ranging behaviour and reproductive capacity (Harcourt et al, 1981). However, variation in social organisation and structure, along with considerable species level variation appears to exist across the genus (e.g. Weidt et al, 2004; Dammhahn and Kappeler, 2005; Lahann, 2008; Génin, 2010).

The significant disparity observed in home range size between sexes in this study is indicative of an extended ranging behaviour in males and a direct strategy whereby males compete for access to receptive females (Trivers, 1972; Emlen and Oring, 1977). However, the dataset does not enable seasonal comparison and it is unclear whether this disparity in home range size is constant throughout the year or is restricted to the reproductive season (September - January). The home range size estimates of *M. tanosi* produced in this study are comparable to a number of other mouse lemur species (e.g. *M. berthae*, *M. ganzhorni* and *M. murinus*) (Radespiel, 2000; Dammhahn and Kappeler, 2005; Lahann, 2008), but notably large compared to others. A study of *M. murinus* in Ankarafantsika showed male ranges increased in size up to an average of ca. 5ha during the reproductive season, whilst female ranges remained constant at ca. 1.8ha. However, an earlier study reported slightly lower estimates (mean male range 3.2ha, mean female

range 1.8ha) (Pages-Feuillade, 1988). Lahann (2008) similarly found the home ranges of male *M. ganzhorni* to be approximately 4.2ha in size in a study predominantly undertaken during the reproductive season, whilst the mean female range size was 0.6ha. The similarity between *M. ganzhorni* and *M. tanosi* is compelling since the two species occupy highly homogenous and proximal habitats, despite being phylogenetically distant relations. Similarly, a study of *M. berthae* demonstrated that male individuals have a mean home range of 4.9ha during the reproductive season, compared to 2.5ha in females (Schwab, 2000; Schwab and Ganzhorn, 2004, Dammhahn and Kappeler, 2005).

In contrast, range estimates for *M. lehilahytsara*, a close relative of *M. tanosi* were lower, estimated at between 0.2 – 0.4ha in males and 0.2 – 0.3ha in females in eastern rainforests (Randrianambinina, 2001). No home range estimates are currently available for *M. rufus* (Atsalis, 2000), another close relative of *M. tanosi*, yet both species occupy similar rainforest habitats and may even overlap in parts of their distribution. Telemetric studies of *M. sambiranensis* have so far reported no difference in home range size between sexes (mean size 1.2ha), however data is currently limited to the non-breeding season (Hending et al, 2017). Likewise, study of *M. ravelobensis* has similarly found no evidence of inter-sex home range size disparity (mean range 0.6ha), either before or during the reproductive phase (Weidt et al, 2004). Furthermore, *M. griseorufus* in Berenty seemingly exhibits an atypical social system, with females occupying significantly larger home ranges than males (Génin, 2010). Although sex-specific data is not available, average range size is small (0.6ha) (Génin, 2008). Whilst the phylogenetic relationships within the genus are not yet fully resolved, the apparent convergence in terms of home range size between *M. tanosi* in Sainte Luce and *M. ganzhorni* in Mandena, and the similarities observed between the sexes is strongly suggestive that environmental conditions play a powerful role in shaping ranging behaviour in mouse lemurs. However, further comparable studies are required to ascertain the degree to which environmental gradients exist and deeper phylogenetic patterns bear an influence. At present, direct comparisons between the available home range estimates are confounded by a number of critical differences in study design (e.g. seasonality, study duration and sample size). Likewise, a range of local ecological factors (e.g. climate, habitat productivity and condition, predator-prey interactions, inter-specific competition) (Clutton-Brock and Harvey, 1977; Goodman et al, 1993; Stokes et al, 2001; Gursky, 2000b) complicate trends and may have also influenced the home ranges estimates produced in this study.

The disparity in observable range estimates between species and sexes may be partially explained by the availability and patchiness of food resources across respective habitats. It has been

postulated that species, including mouse lemurs compensate for food scarcity by increasing their foraging areas (Emlen and Oring, 1977; Harvey and Clutton-Brock, 1972; Tew and Macdonald, 1994; Lurz et al, 2000; Dammhahn and Kappeler, 2005). Such strategies have been observed in other primate species including squirrel monkeys and spectral tarsiers (Boinski, 1987; 1988; Gursky, 2000b) and it is thought to be more pronounced in females, given their home range size is predominantly determined by the distribution of resources. Since mate searching is an important additional component of male ranging behaviour, female ranging patterns then influence male strategies (Radespiel, 2000; Dammhahn and Kappeler, 2005). Although the southeastern littoral forests do not experience any pronounced climatic extremes compared to other areas of the island (Jury, 2003; Vincelette et al, 2007c), phenological studies have shown a highly synchronised temporal clumping of fruit resources (Bollen and Donati, 2005), coinciding with the austral summer, the reproductive season for mouse lemurs. This may explain the similarity in ranging behaviours observed between littoral *M. tanosi* and *M. ganzhorni* populations.

During periods where resources are relatively abundant, efficient female foraging may result in smaller home ranges, whilst males may expand their ranging area in search of female partners, unhindered by limited food resources. Indeed, 50% FK analysis found no difference in core home range area between the sexes, further suggesting that larger male ranges are extensions related to reproductive drive rather than resource acquisition. A complimentary investigation into the home range size of *M. tanosi* during the austral winter may provide increased clarity on the factors influencing mating strategies. Similarly, physiological strategies adopted to survive periods of reduced resource availability and extremes in temperature can potentially also lead to differences in home range size (Dammhahn and Kappeler, 2005). Although rare amongst primates, a number of mouse lemur species are known to be able to enter a torpid state (Petter, 1978; Petter-Rousseaux, 1980; Ortmann et al, 1996; Schmid, 1996; Schmid and Kappeler, 1998; Atsalis, 1999b). However, the extent and duration of metabolic suppression appears to be both species and habitat-specific (Schmid et al., 2000; Schmelting et al, 2000; Lutermann and Zimmermann, 2001; Atsalis, 2008) and at present, the capacity of *M. tanosi* to undertake temporary bouts of torpor is unknown, and its effect on sex-specific home range size is also unclear.

In this study, the high degree of range overlap, both between focal males and females, indicates a lack of consistent territoriality, especially between males, and confirms that all focal animals (adults) had spatial access to multiple potential mates. Even within this limited sample, there appears to be no evidence in support of the spatial dominance of females by specific male individuals, consistent with other studies (Radespiel 2000; Weidt et al, 2004; Lahann, 2008;

Hending et al, 2017). Similarly, no evidence for a female dominance structure within localised range nuclei was discernible (Martin, 1973). Whilst temporal home range stability could not be addressed in this study, studies on *M. murinus* have shown that some degree of inter-seasonal stability exists (Radespiel, 2000), and that close associations are linked to genetic relatedness (Radespiel et al, 2001b). However, the limited battery life of the lightweight radio-collars precluded continuous year-around or multi-year assessment and not all animals in the study area were tracked. Yet from the limited data available it may be concluded that 'scramble' competition presents the most parsimonious explanation for the distribution of study individuals. Whilst this system seems fairly ubiquitous in mouse lemurs, albeit with notable exceptions (Weidt et al, 2004; Génin et al, 2010), it also has wider precedent in Madagascar's lemurs, and has also been reported in both *Mirza coquereli* and *Daubentonia madagascariensis* (Sterling, 1993; Kappeler, 1997b).

Results from both the MCP and FK methods are mostly consistent in this study, but differ in magnitude, with FK analysis generating smaller home range and overlap estimates. Notably however, the two methods produce disparate results with regards to how both sexes utilise their ranges. Based on MCP data, female individuals were found to select sleeping sites closer to their home range centres than males, suggesting a more conservative and risk adverse use of their mapped territories. Males, meanwhile, appear to accept the risks associated with exploring more widely in search of females (Kraus et al, 2008). However, this result was not confirmed based on FK range data, and instead females were found to select sleep sites nearer to the boundaries of their range. This is likely an artefact of the home range estimation methods, with both MCP and FK analysis drawing home range boundaries based on fundamentally different principles (Harris et al, 1990). A further caveat when considering the accuracy of home range estimations, is the underlying dataset from which they are generated. In this study, a variable number of localities (GPS fixes) were obtained for each individual due to variations within activity level during the nocturnal follows, and the length of the study period over which the animal could be tracked. As visual confirmation of the precise location of the focal animal was preferred over a regular time-interval recording method, the number of data points collected over the course of a follow was un-equal. Whilst a continuous time-based sampling method was initially trialled, maintaining close contact with the focal individual in dense forest was often very difficult, and observations at specific times could not be reliably attained. Furthermore, over the course of the study, a number of focal individuals either escaped from their collars (n=3), went missing entirely (possibly predated, or dispersed) (n=1), or were discovered deceased (n=2), resulting in reduced individual datasets.

Similarly, the number of sleeping site fixes was uneven between focal individuals, primarily as a result of the difficulties associated with captures. It is also clear that the home range estimates of some individuals are based on too few data, determined by IAA analysis, and likely represent an incomplete image of an individual's true range. However, efforts have been made to account for these discrepancies using statistical methods. Although each of these factors will have impacted the final home range estimates to some degree, the output represents the best possible utilisation of the data based on careful analysis and modelling of both MCP and FK ranges. Furthermore, the home range estimates appear comparable with those published for other mouse lemur species studied so far, although indicate that *M. tanosi* has one of the largest known home ranges.

It is also important to note that many additional uncollared mouse lemur individuals were sighted during both study periods and it was common to observe focal animals sharing sleeping sites with multiple uncollared animals. As a consequence, the results presented in this chapter represent only a small portion of the true extent of social interactions between individuals within the study area. It is highly likely that the social neighbourhood extends throughout the study fragment and that all individuals are in some contact with con specifics. Whilst it is reasonable to assume that the number of mouse lemurs each individual encounters may vary across any given area (i.e. some localised population density gradients may exist), perhaps governed by specific habitat characteristics (Rendigs et al, 2003; Schwab and Ganzhorn, 2004; Andrianasolo et al, 2006), the disconnect of a single focal individual in this study is likely an arbitrary artefact of the capture methodology and limited sample size. Whilst there is no reason to suspect any gap in population continuity within the study forest fragment, with *M. tanosi* considered a species relatively tolerant of moderate habitat disturbance (Andrianasolo et al, 2006), the effect of sharp habitat edges is unclear, and likely species specific (Ganzhorn and Schmid, 1998; Rendigs et al, 2003; Andrianasolo et al, 2006; Lehman et al, 2006; Randrianambinina et al, 2010; Steffens et al, 2016). Anecdotally, the study area was chosen specifically due to the high number of opportunistic mouse lemur observations, possibly related to the soft habitat edge and secondary forest gradient.

Whilst the broad evidence presented in this chapter identifies scramble competition as the prevailing mating system, the degree to which more subtle dominance behaviours and strategies interplay is less clear. The body mass of focal individuals was only measured once, following initial capture, due to the difficulties and stress factors associated with regular recapture by hand. As such, the relationship between mass and home range size, an important marker for reproductive dominance under the 'contest' hypothesis (Trivers, 1972; Kappeler and Van Schaik, 2002) could not be reliably determined. Similarly, the low number of focal male individuals in

the study precluded any robust correlational analysis between body mass and range size. Whilst no evidence for sexual dimorphism was found across a range of salient biometric traits (e.g. body mass, body size, canine length), an indication that male physical dominance is not a key determinant in reproductive success, testicular volume was pronounced during the reproductive period (see **Chapter 3**). Large testicular volume, relative to body mass is widely acknowledged as strong evidence for the existence of sperm competition within *Microcebus* spp. (Glatston, 1979; Kappeler, 1996; Fietz, 1999; Radespiel; 2000; Schmelting et al, 2000; Schwab, 2000; Wrogemann and Zimmermann; 2001). Furthermore, a range of additional subtle and sex-specific reproductive strategies may exist, with conflicting strategies influencing expressed ranging behaviours.

Whilst temporary mate guarding has been reported in captive populations of *M. murinus* (Perret, 1992; Wrogemann et al, 1997), it was not observed during this study. Given the very brief window of receptivity in female mouse lemurs (Lebec, 1984; Blanco, 2011), such a strategy could be worthwhile and successful for males (Radespiel, 2000). However, further high-resolution behavioural study would be necessary in order to demonstrate the existence of such behaviour in the wild. Again though, the distinction between behaviour observed in the wild and in captivity are likely important, as the underlying factors (e.g. time access to mates and proximity to competitors) that determine how intra-sexual reproductive strategies manifest are altered. However, given that the intra-population variation within female estrous is relatively broad (Eberle and Kappeler, 2002; Blanco, 2011), mate guarding is a highly plausible strategy. Reports of males waiting for females to emerge from sleeping sites before attempting to mate with them has been reported (Radespiel, 1998), however since sleeping sites in *M. tanosi* appear to change frequently (likely on a nightly basis), the predictability of where an individual may be located is limited. Additionally, the cognitive ability of individual males to spatially map the location of female home ranges and the specific locations of favoured sleeping sites may represent important fitness advantages and drive invisible competitive hierarchies. The short temporal window of female receptiveness should also drive competition between males to recognise and react to sexual advertisement by females. Increased marking frequency and the use of specific calls by females (Buesching et al, 1998) provides information to potential mates, and the ability of individuals to both produce and detect signals likely impacts on fitness and represents a component of a broader reproductive strategy. The factors that govern female mate selection in mouse lemurs are still poorly understood and complicated by the limited time frame available to select mates and the necessity to breed early in the season to coincide with peak seasonal resource abundance (Bollen and Donati, 2005). Parental investment in mouse lemurs appears to be exclusively undertaken by females, therefore mate selection should be an important consideration (Bateson, 1983). Given

that all focal animals in this study likely had access to multiple potential partners, further investigation into the mechanisms of mate selection in the wild is required. However, some studies indicate that females are not selective during peak estrous (Radespiel, 2000; Eberle and Kappeler, 2002) and male strategies ultimately determine the reproductive system of the species. Conversely, proximal individuals likely recognise each other (Radespiel, 2000) and therefore preferential mating may be established prior to estrous.

In addition to the modelled home range estimates and depiction of the social mode of *M. tanosi*, important insights may be gained from specific interactions and inter-individual associations. Regardless of their subsequent ranges, all focal animals in this study, except for a single male were captured within an area of secondary forest 15ha in size. Whilst in a number of cases the capture sites were omitted as anomalous ranging localities, the realisation that all focal individuals visited this specific area within the study period indicates that certain areas may attract large numbers of mouse lemurs. In this case, the area was characterised as being relatively degraded (includes a plant nursery and the main entrance to the forest fragment), with a low density of large trees (88.5/ha with DBH>5.25cm), low canopy height (mean=6.4m) and composed mainly of edge tolerant tree species. It is possible that the area provides an important feeding site for mouse lemurs, with increased resource availability (Corbin and Schmid, 1995; Ganzhorn et al, 1995; Bollen and Donati, 2005; Lehman et al, 2006) or alternatively constitutes an important area for social purposes. Furthermore, the estimated home range size of two male individuals in the study are notably larger than the others. They also show the greatest percentage of inter-male range overlap (56.8% overlap using adjusted MCP estimates or 45.8% using 95% fixed kernels) and both ranges cover a large proportion of the seemingly favourable capture area. Whilst it is possible that these large ranges are artefacts of the limited male sample size, it is also possible that these territories belong to high-status individuals, able to dominate larger areas due to traits or behaviours associated with increased fitness (e.g. urine marking, increased advertisement call frequency or high levels of aggression) (Perret, 1992; Perret and Schilling, 1995; Perret et al, 2001; Craul et al, 2004). Similarly, the home range overlap of two sets of females is extremely high (67.9% and 75.8% under adjusted MCP estimates) and may indicate the presence of matrilineal range nuclei (Radespiel et al, 2001b). However, the percentage overlap is greatly reduced in the fixed kernel estimations.

Although the full picture of mouse lemur sociality is not yet entirely developed, this study adds to the known behavioural ecology of the genus, and the species-specific variation exhibited within it. *Microcebus tanosi* appear to have relatively large home ranges compared to some other studied

species, although displays important continuity with others, with males ranging over significantly larger areas than females, at least in the reproductive season. The species also conforms to the social model of a dispersed, but individualized neighbourhood system, characterised by substantial inter and intra-sexual home range overlap (Radespiel, 2000). This study finds no evidence of the spatial monopolisation of females by dominant males, but instead supports the scenario whereby male competition for access to fertile females is principally manifest through 'scramble' competition. In the specific context of Sainte Luce, insight into the social structure and organisation of *M. tanosi* could be crucial in the development of informed conservation strategies, particularly given the highly fragmented nature of the existing forest. The remaining littoral forest fragments in Sainte Luce currently face a variety of existential environmental threats, including on-going habitat loss as a result of resource extraction and agricultural expansion (Bollen and Donati, 2006 and see **Chapter 7**) and proposed mining operations (QMM, 2001; Temple et al, 2012). As such, a robust understanding of how key Endangered species such as *M. tanosi* utilise the littoral environment can help to mitigate and minimise the impacts of environmentally damaging activities. It is also becoming ever-clearer that safeguarding key seed-dispersing species such as lemurs is crucial for the success of long-term environmental strategies (Chapman, 1995; Chapman and Onderdonk, 1998; Levey et al, 2002; Bollen and Donati, 2006; Lahann, 2007; McConkey et al, 2012; Chapman and Dunham, 2018; Ramananjato, 2020).

CHAPTER 5

Sleeping site and nest ecology

Background

The necessity for sleep is a universal behaviour among all animals (Lesku et al, 2006; Hartse, 2011) and the selection of a safe sleeping position is a critical consideration from a Darwinian perspective. For all primate species, a suitable shelter can provide both protection from extreme environmental conditions and security from predators (Hamilton, 1982; Anderson, 1998; Kappeler, 1998; Cheyne et al, 2012; Fichtel, 2012; 2016). However, it is now becoming increasingly evident that sleep site selection also impinges on less obvious factors such as parasite load, pathogen transmission and cognitive function, which can all negatively impact individual fitness (Chapman, 1989; Rahman et al, 2013; Samson et al, 2015; Samson and Nunn, 2015; Fruth et al, 2017; Hokan et al, 2018). The position of the sleep site is also mediated by ecological factors such as niche availability, the distance to desired foraging areas, and social factors such as inter species competition, group composition and ranging behaviours (Chapman, 1989; Anderson, 1998; Lahann, 2007; Biebouw et al, 2009; Seiler et al, 2013). Thus, selecting a suitable sleeping site is a complex decision that must balance each of these aspects. To date, a wide variety of sleep sites and nest types have been reported in primates, including inside tree holes, in tree crowns and tree forks, constructed foliage nests, cliff faces, caves, rocky outcrops and even anthropogenic structures (Lutermann et al, 2010; Semel and Ferguson, 2012). Hibernation has even recently been reported underground in a nocturnal lemur (Blanco et al, 2013). Similarly, a range of social sleeping configurations have been observed within the order, ranging from semi-stable sleep cohorts (often comprising familial groups or dyads) as in some *Eulemur* species and wooly lemurs (*Avahi* spp.), variable group sharing as in Barbary macaques (*Macaca sylvanus*) and some mouse lemurs species (*Microcebus* spp.) to solitary sleep behaviours as observed in slow loris (*Nycticebus* spp.) and orangutan species (*Pongo* spp.) (e.g. Hamilton, 1982; Anderson, 1998; Kappeler, 1998; Radespiel et al, 2003b; Samson and Shumaker, 2015; Svensson et al, 2018).

Whilst it is well established that sleeping and nesting sites are a reflection of underlying behavioural adaptations and that broad genus level trends exist (Kappeler, 1998; Bearder et al, 2003; Svensson et al, 2018), fine-scale variation occurs at species level. Given that sleeping

behaviours comprise an important aspect of a species' overall social organisation and social system (Bearder, 1987; Kappeler, 1997b; Muller and Thalmann, 2000; Kappeler and van Schaik, 2002), insights into this domain are crucial to understanding a species' social mode. Over 50% of extant primate species are nocturnal and given the explosion of recognised forms in recent decades, the data pertaining to the sleeping ecology is lacking for many taxa. Despite this, the general structures utilised are fairly well known (Kappeler, 1998; Bearder et al, 2003; Svensson et al, 2018), however, in many cases our understanding of the physical characteristics and ecological drivers of site selection remains fragmentary. Nest building behaviour is believed to have evolved between six to eight times independently in primates (Kappeler, 1998), and although often associated with the Great Apes (Goodall, 1962), it is also considered an ancestral trait of the strepsirrhine suborder (Martin, 1972). The construction of nests provides a multitude of explicit benefits over open sleeping sites, particularly in the context of lemurs (Kappeler, 1998).

In theory, a nest site provides concealment and restricts access to predators, whilst affording thermoregulatory benefits by providing insulation from outside conditions. As a result, nest building is regarded as a form of behavioural thermoregulation (Fruth et al, 2018) and appears particularly important for small and solitary species (Charles-Dominique and Martin, 1972). Nests also provide shelter for altricial young (Radespiel et al, 1998; 2003b; Schmid, 1998) and are considered particularly important for nocturnal strepsirhines (Kappeler, 1998). Based on phylogenetic reconstructions, Kappeler (1998) further proposed that the sheltering of neonatal young was likely the primary driver behind the origin of nest construction in early primates. Given the importance of nests then, the specific location of a nest site should be a critical matter. Indeed, chimpanzee (*Pan troglodytes*) nests are typically built at greater heights, in closer proximity and in trees with defensive characteristics in areas with higher predation pressure (Hernandez-Aguilar, 2006; Pruetz et al, 2008; Stewart and Pruetz, 2013). Humidity avoidance has also been demonstrated as a determinant influencing chimpanzee nest site location (Koops et al, 2012), indicating a strong thermoregulatory component (Bell and Greene, 1982) or alternatively a strategy to reduce disease vector prevalence (Heymann, 1995; McGrew, 2004; Largo et al, 2009; Samson et al, 2013). However, it is important to note that the majority of nest related studies have so far focused on great apes and it is unclear to what extent nesting attributes are shared amongst other taxonomic groups.

Tree holes similarly provide all of the benefits of nests, offering important places to shelter from harsh environmental conditions and cover from predators. They are commonly reported as sleeping sites for primates, although most notably amongst small to medium sized nocturnal

species (Kappeler, 1998; Schmid, 1998; Fietz, 1999; Bearder et al, 2003; Fichtel, 2016, Svensson et al, 2018). Larger species are seemingly precluded, limited by space, and haplorrhine species appear to only rarely use them (Kappeler, 1998; Bearder et al, 2003). Whilst self-constructed nests have relatively little limitation in terms of where they can be made, since natural building materials are often abundant, tree holes conversely are a fixed and often limited resource. Whereas nests can be constructed and positioned optimally to exploit resources, for defensive or territorial purposes, well positioned tree holes are likely the source of considerable competition. However, tree holes can provide better insulation properties than either leaf nests or open branch and foliage sites (Weidt et al, 2004; Daumann et al, 2005; Kobbe and Dausmann, 2009; Nowack et al, 2010). As a result, tree holes clearly provide important refuges for many primate species, particularly in dry or cold seasons (Ortmann et al, 1997; Kappeler, 1998; Bearder et al, 2003; Radespiel et al, 2003b; Dausmann et al, 2004; Rasoazanabary, 2006). Furthermore, larger tree holes can allow for multiple occupancy and facilitate additional social thermoregulatory behaviours such as huddling and close contact. Such behaviours convey energetic advantages to co-habiting individuals over those who opt to sleep in solitary (Perret, 1998; Schmid, 1998), with the average ambient temperature of a shared sleeping site increasing with the number of occupants (Charlot and Perret, 2000). Therefore, access to such sites may infer survivorship benefits during cold conditions. Cohabitation further provides opportunity for social interaction and bonding (Armitage, 1998; Blumenstein et al, 2004), however, close conditions may also facilitate the transmission of ectoparasites and disease (Anderson, 1998; Hokan et al, 2017).

Despite the manifold benefits of nests and tree holes, many nocturnal primate species opt to sleep in more open sites, either in tree forks, amidst dense tangles of vegetation or in tree crowns (e.g. Kappeler, 1998; Bearder et al, 2003; Wiens and Zitzmann, 2003; Gould and Sauther, 2007; Nekaris and Bearder, 2007). Whilst individuals choosing open sites still face similar constraints to those in other sleep site types (e.g. risk of predator detection and meeting thermoregulatory requirements), there are some advantages. Firstly, open foliage sites are plentiful in forest habitats and so competition is relaxed, enabling individuals to frequently change sleeping site, reducing predation risk. Given that sleeping site localities are governed to a large extent by ranging behaviour and territoriality (Anderson, 2000), the use of open sleep sites may provide an opportunity to rest in strategic areas, in the territory of others if pursuing a mate, or to exploit ephemeral resources. Furthermore, comparatively little investment is required, either through engaging in competition with rivals or in nest building activities. However, open sites offer little security to neonates or vulnerable adults. Theoretically then, it could be expected that females select sleep sites in a more cautious manner than males (Trivers, 1972; Emlen and Oring, 1977)

and indeed, there is evidence for sex-specificity amongst solitary species (Radespiel et al, 1998; 2003). Furthermore, the reduced insulation capacity of open foliage sites means that the effects of thermal stress must be mitigated in other ways (e.g. by physiological adaptation or thermoregulatory behaviours such as cohabiting, huddling or curling up) (Müller et al, 1985; Schmid and Ganzhorn, 1996; Dausmann et al, 2004).

The nocturnal lemurs of Madagascar represent an exceptionally speciose community of primates (Mittermeier, 2010) and an ideal model taxa to study the complexities of sleep site ecology. Notable amongst these are the Cheirogaleidae (comprising five genera; *Cheirogaleus*, *Microcebus*, *Mirza*, *Phaner* and *Allocebus*), for whom selecting a suitable sleeping site is particularly crucial. Several members of this group are known to enter periods of daily torpor or undergo bouts of seasonal hibernation (Ortmann et al, 1997; Schmid and Kappeler, 1998; Schülke and Ostner, 2007; Dausmann et al, 2004; Blanco and Rahalinarivo, 2010; Blanco et al, 2013). The genus *Microcebus* represents a particularly salient and speciose genera, currently comprising 26 recognised species and distributed across all of Madagascar's forested habitats. However, the sleeping ecology of just eight species has so far been investigated (**Fig. 23**). Nesting and sleep site selection should be particularly crucial for *Microcebus* spp., given their trophic position, as highly vulnerable prey species with a variety of nocturnal and diurnal predators. Several species are known to enter daily torpor and can hibernate through harsh seasons (Schülke and Ostner, 2007). Mouse lemurs like many nocturnal primates, occupy dispersed but individualised social neighbourhood systems (Atsalis, 2000; Radespiel, 2000; Weidt et al, 2004; Dammhahn and Kappeler, 2005; Génin, 2010; Hending et al, 2017), where individuals are familiar with those whom they share their sleeping sites with and whose ranges overlap (Struhsaker, 1969; Radespiel, 2000 and see **Chapter 4**). Understanding behaviours associated with sleeping sites, such as group composition and spatiotemporal cohesion is particularly important in species whose social interactions are often displaced (Eisenberg et al, 1972; Bearder, 1987; Martin, 1995; Hohenbrink et al, 2012) and may reveal insight into otherwise hidden social structure.

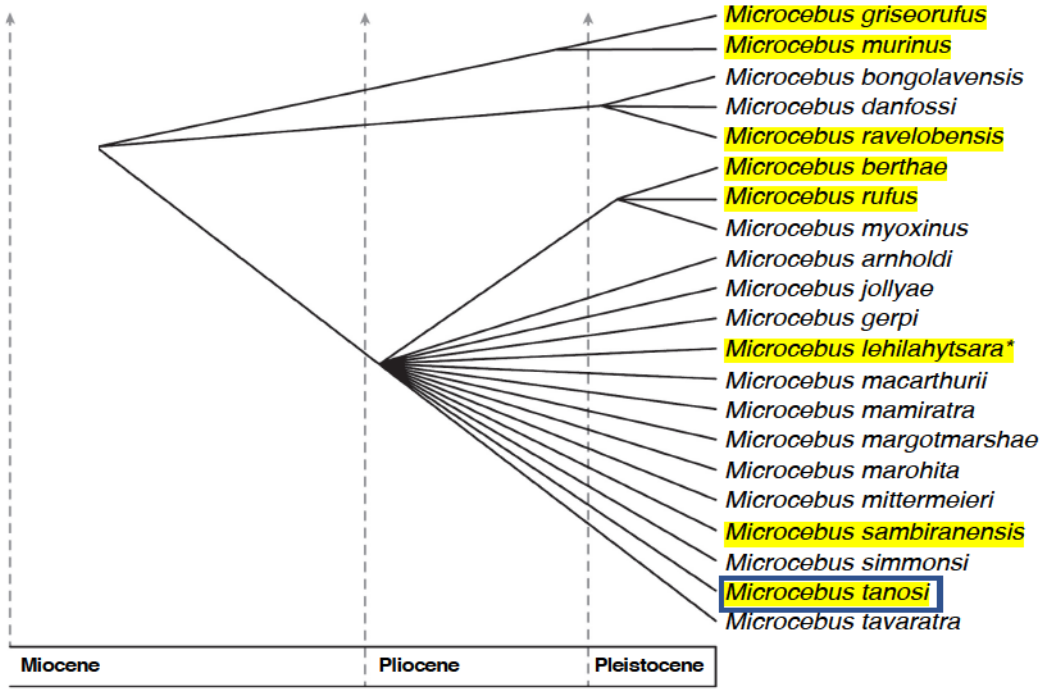

Figure 23 – Phylogenetic relationships within *Microcebus*. Branches scaled proportionally to time. Figure adapted to highlight species whose sleep site ecology has been studied. *Studied in captivity. **This figure does not include the 5 most recently described species (Hotaling et al, 2017; Schüßler et al, 2020).

Although scant, the available literature indicates that *Microcebus* species are relatively flexible in terms of the structures they use as sleeping sites (**Table 16**), utilising leaf nests and tree holes to more impromptu localities such as the disused bird nests, fallen vegetative debris and even spaces beneath spider webs at ground level (Schwab, 2000; Radespiel et, 2003b; Génin, 2010). However, trends and direct species comparisons are complicated by the wide range of different environments that species occupy across Madagascar (Mittermeier et al, 2010). Furthermore, studies vary in duration, season and the number of focal individuals, serving to stymie any fine-scale trends. However, it does appear that broad patterns exist, and the majority of sleep site observations fall into two general categories: tree holes and open foliage sites. It is notable that some species show a clear preference for either tree holes (e.g. *M. murinus*), or foliage sites (e.g. *M. berthae*, *M. griseorufus*, *M. sambiranensis*) whilst others seem to show more proportionate usage (*M. ravelobensis*) or even sex-specific differences (*M. ganzhorni*). Until now only *M. ganzhorni* has been demonstrated to show such sex-based disparity (Lahann, 2008), but is one of the few studies to examine almost year-round data, hinting that seasonality may play a critical role in determining sex-specific strategies.

Table 16.

A summary of all known sleep site structure data for *Microcebus* species. 'Various other' represents a miscellaneous category for sites that do not fit into the broader categories. These include the abandoned nests of other species in the case of *M. berthae* and *M. griseorufus*, fallen tree debris and leaf deposits on the ground in *M. berthae*, *M. murinus* and *M. ravelobensis*, beneath tree bark and spiders' webs in *M. murinus* and *M. ravelobensis* and in a tree fork in *M. ravelobensis*. *Indicates a captive study.

Species	Sleeping Sites	Reference
M. berthae	Foliage sites (79%), Tree holes (10.5%), Various other (10.5%)	Schwab, 2000
M. ganzhorni	Tree holes (♂ 15%; ♀ 78%), Pandanus sp. (♂ 6%; ♀ 18%), Open Foliage (♂ 79%; ♀ 4%)	Lahann, 2007
M. griseorufus	Vine tangles (25%), Alluaudia (36%), Euphorbia (30%), Hollow branches (7%), Various other (2%)	Génin, 2010
M. lehilahytsara	Foliage sites (*Pandanus* spp 85.9% of cases)	Jürges et al, 2013*
M. murinus	Tree holes (85.9%), Various other (12%), Foliage sites / Branches (2.2%)	Radespiel et al, 2003
M. ravelobensis	Tree holes (46.2%), Foliage sites / Branches (28.2%), Various other (25.6%)	Radespiel et al, 2003
M. rufus	Tree holes and Foliage sites (%'s unspecified)	Karanewsky & Wright, 2015
M. sambiranensis	Foliage sites (93%), Tree holes (7%)	Hending et al, 2017

Given the social importance of sleeping sites, understanding interactions at these localities is of great utility and may reveal species-specific behavioural adaptations that underpin mouse lemur societies. All mouse lemur species studied to date exhibit a promiscuous mating system, with most characterised by 'scramble competition' (Kappeler, 1997; Radespiel, 2000; Kraus et al, 2008). Yet the interaction between the sexes at sleeping sites appears divergent and even varies between populations. Whilst a wide variety of sleeping group configurations have been reported, including temporally stable groups of closely related females, same sex pairs and groups, solitary individuals and mixed male-female groups (Radespiel et al, 2003; Weidt et al, 2004; Lahann, 2008; Génin, 2010; Thorén et al, 2011; Jürges et al, 2013), such observations are consistent with the differentiated reproductive strategies of the sexes and an individualised neighbourhood social system (Trivers, 1972; Emlen and Oring, 1977; Clutton-Brock, 1989; Clutton-Brock and Parker, 1992; Sterck et al, 1997 and see **Chapter 4**). However, relatively few studies compare seasonal data and robust inter-species social comparisons are so far largely precluded, as are any broader trends within the genus.

Whilst the general architecture used by mouse lemurs for sleeping and nesting is largely understood, less is known about the specific physical and microhabitat characteristics of the sites. Studies on those species known to enter bouts of daily torpor have revealed that individuals select larger diameter trees, interpreted on the basis that larger trees have greater insulative qualities

(Schmid, 1998; Génin, 2010; Luttermann et al, 2010). Radespiel et al (1998) also found female mouse lemurs occupied larger and better insulated tree holes than males in Ankarafantsika National Park and were also positioned higher in trees. Some evidence also suggests that *M. rufus* at Ranomafana National Park select comparatively larger or taller trees as sleep sites, depending on habitat quality, with taller trees used in degraded areas where larger trees were missing (Karanewsky and Wright, 2015). Sleeping site selection may be particularly crucial in disturbed and degraded forests, where resources are limited and canopy cover is reduced, potentially increasing ambient temperature above the threshold required for torpor (Ganzhorn and Schmid, 1998; Schmid, 1998; Kobbe and Dausmann, 2009). Conversely however, a study investigating sleep site selection in *M. sambiranensis* found no difference in the sleep site characteristics between individual study animals or sexes (Hending et al, 2017).

At present, *M. tanosi* represents an unstudied species, with no information available with regards to its sleeping and nesting behaviour. Whilst it almost certainly fits within the broad parameters that frame mouse lemur socioecology, improving our understanding of species-specific social behaviour will further add to the available data for the genus. Likewise, it offers an opportunity to compare the sleeping and nesting habits with those of other studied species, most notably *M. ganzhorni*, which despite being a relatively distant genetic relative, shares a homogenous and proximal environment. Like all mouse lemur species, *M. tanosi* constitutes an important link in the ecosystem, serving as both predator and prey species. Mortality rate is currently unknown but is likely to be high and may be comparable to that of *M. murinus* at ca. 25% per year (Goodman et al, 1993). As a result, it could be expected that *M. tanosi* expresses a variety of behavioural strategies to counteract those employed by local predators (see **Chapter 2**, **Predators**). If predator avoidance is a key factor in sleep site selection, it could be expected that individuals will change sleeping site frequently, share sleep sites as often as possible and select sites with good defensive attributes. Alternatively, if individual *M. tanosi* are selecting sites in line with thermoregulatory demands, it could be expected that individuals habitually select sites with good insulative properties, i.e. tree holes within large mature trees, and in shaded areas away from the forest edge and within intact areas of forest. Furthermore, it may be expected that individuals would compete for sites and show a high degree of site fidelity, changing sites infrequently.

The principal aim of this study is to investigate the sleeping and nesting habits of *M. tanos*i in a littoral forest habitat, characterise the general structures used, and to determine which ecological factors are most important in site decision making. Identification of the primary factors governing sleeping site selection will not only add to the overall understanding of the genus, facilitating

inter-species comparison, but will provide a deeper insight into the drivers influencing an important aspect of mouse lemur behaviour. Furthermore, the findings of this investigation may be important for local conservation efforts. In order to meet these aims, the following research questions are addressed:

1) What general habitat structures characterise the sleep sites of *M. tanosi*?
2) Is there any evidence for differentiated sleep site selection between sexes?
3) To what extent do individuals and sexes share sleep and nesting sites?
4) What ecological forces are driving sleep site selection in Sainte Luce?
5) Does the sleep site selection of *M. tanosi* differ from that observed in other mouse lemur species, and can any broad patterns be detected?

Based on available literature, the following hypotheses are proposed:

1) The general habitat structures used by *M. tanosi* will be similar to those utilised by other *Microcebus* species in similar environments (e.g. at other littoral sites and in proximal eastern rainforests) i.e. a mix of open foliage type sites and tree holes.
2) Males engaged in intra-sexual scramble competition for mates are more likely to select sub-optimal sleeping sites than females and so sex-specificity in sleeping site selection is expected.
3) Sleeping cohort stability will be low if predator avoidance is a major factor influencing sleep site selection. Similarly, female group associations are expected to be more stable than those of males, if female *M. tanosi* conform to the same matriarchical social structures observed in other species.
4) Predator avoidance will constitute the predominant force governing sleeping site and nest site selection, rather than thermoregulatory considerations, given that the southern littoral forests lack the extreme climate seasonality of other localities in Madagascar.
5) The sleeping sites selected by *M. tanosi* will be largely similar to those of other eastern species studied so far, modulated subtly by specific local environmental conditions.

This study took place in littoral forest fragment 'S9' in Sainte Luce (see **Chapter 2, Study area**) across two main periods, between August 2017 and January 2018 and August 2018 to November 2018. The study coincided largely with the austral summer and with the known reproductive period of the focal species (October – January). A range of standard methods were used to collect weather data across the study period. A digital rain gauge measured monthly precipitation, whilst two in-situ HOBO Pro V2 temp/RH data loggers recorded hourly temperature and humidity. Climate data is provided in **Figure 24**.

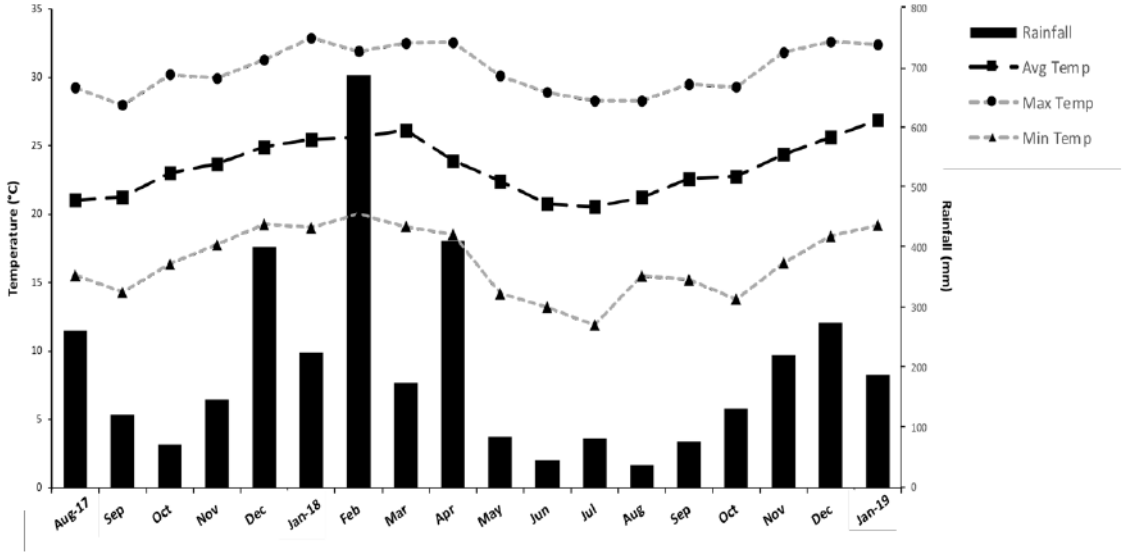

Figure 24 – Monthly rainfall and temperature patterns in Sainte Luce across an 18month period. The highest recorded temperature was in January 2018 (32.9 °C) and the lowest in July 2019 (13.2 °C). Temperatures were recorded within the forest interior and so represent values experienced by the study lemurs.

At the beginning of each study period a number of individual mouse lemurs were trapped and fitted with HOLOhill PD-2C very high frequency (VHF) radio collars (see **Chapter 2**, **Radio-collaring**). Throughout the study, a total of 23 focal individuals (9x ♂, 14x ♀) were located at their sleep sites during the day. Animals were tracked by SHR using standard telemetry techniques (Honess and MacDonald, 2003). Equipment consisted of a Lintec flexible 3-element directional yagi antenna (150 MHz; 148.000MHz – 151.999MHz) and AOR 8200 wide range receiver, a

Garmin GPSmap 62s and a pair of Swarovski 8-42 SLC HD binoculars. Once in the immediate vicinity of the lemur, as indicated by the telemetry equipment, the immediate vegetation was scrutinised in order to observe the concealed primate. Data collected was dependent on whether the animal could be directly observed or not at the sleep site. If visible, the observation was treated as a 'confirmed sleep or nest site' and the following information was recorded; GPS point (accurate to 3m), sleep site type, tree species if applicable, animal height, tree height, diameter of the tree at breast height (DBH), canopy cover, canopy height, crown diameter, elevation, sleep site cohort and an accompanying assessment of the forest density using the Point Centred Quarter (PCQ) method (Cottam and Curtis, 1956). Also, at a confirmed sleep site, the signal of all other study animals was checked to determine whether the sleep site or nest was being co-occupied by other collared animals.

The presence of additional uncollared animals was not actively investigated beyond visual inspection, minimising disturbance to the site and preventing potentially disrupting the lemur's future site selection or increasing its predation risk by forcing it to abandon the site. If the focal animal could not be observed at the sleep site location after 20 minutes of scanning but was clearly within close proximity (<10m), as indicated by the telemetric equipment, the observation was treated as a 'approximate sleep site' and only the GPS position was recorded. Occasionally, the animal could not be observed directly but the highly directional antenna could pinpoint a specific sites that likely concealed the lemur (e.g. a particular *Pandanus* screwpine or an obvious tree hole). In such circumstances, a reduced set of data was recorded (GPS, sleep site type, tree species, tree height, DBH and canopy height), however it was still recorded as an 'approximate sleep site' to distinguish the observation from those where the lemur was confirmed. If no signal could be detected after one hour of searching for a signal for a focal animal, the observation was classified as 'no signal' and the lemur was presumed missing or outside of its usual territory. On a number of occasions, the remains of a study animal were discovered (n=2), collars were recovered after being dropped (n=4), no signal was detected (n=35) and equipment malfunctioned (n=2).

Individual study animals were tracked to their sleep or nest sites three times a week during periods of active field research, but the exact number of visits was dependent on weather conditions. Telemetric work was always carried out during the morning, between 08.00am and 10.00am. During each observation, the tree species used for resting were identified in the field by expert local field guides. Vernacular names were later cross referenced with published resources and a herbarium of botanical samples identified by staff at Kew Gardens and Missouri Botanical Gardens in Antananarivo (see **Chapter 2**, **Botanical assessment**). Sleep sites were classified into

the following general categories; Leaf nest, Tree hole, Canopy foliage, *Pandanus* and Other (**Table 17**). The height of the exact sleep site (location of the lemur) was estimated to the nearest metre by SHR, along with the height of the tree and the top of the canopy directly above the lemur. Binoculars were used to ascertain whether the lemur was alone or sharing the sleep site or nest, and the maturity status and sex of any associated individuals where possible. Canopy cover or closure was determined using a standard densiometer (*Forestry Suppliers Convex Model A*) (Lemmon, 1956; Korhonen et al, 2006), with measurements taken directly below the resting lemur. Four readings were recorded for each locality and an average was recorded.

Table 17.

The definition of each broad sleeping site category used in this study. Combined, the categories Leaf Nest, Canopy foliage, Pandanus and Other all represent foliage sites. The category 'Pandanus' refers specifically to the leaf axils of *Pandanus dauphinensis* and *Pandanus concretus* and is treated as a separate category from Canopy Foliage due to the plant's unique properties and frequent use.

Type	Description
Leaf nest	A constructed spherical nest made from collected leaves, often centered around a thin branch.
Tree hole	A natural space or hollow within a tree.
Canopy foliage	An exposed location within the branches and leaves of a tree.
Pandanus	A specific palm-like species of screw-pine with defensive characterstics. See **Fig. 28 E-H**.
Other	A miscellaneous category that includes a variety of unusual localities, such as epiphytes and amidst fallen leaves.

The PCQ method was used to describe the horizontal vegetation structure or density (Brower et al, 1990; Ganzhorn et al, 2008) of a sleeping site. The sleeping or nesting position of the lemur was used as the central point, and the distance to the centre of the nearest tree with a minimum circumference value at breast height of 12.5cm (DBH $\geq$ 4cm) was recorded for each of the four compass quarters (NW, NE, SW and SE). A low minimum tree circumference was chosen as mouse lemurs are known to utilise small shrubs and bushes as well as trees (Andrianasolo et al, 2006). The density of trees per unit area was then calculated using the equation below. Tree height, DBH and tree species were also recorded for each directional quarter.

$$\text{Density } (\textit{all species}) = \frac{1}{\text{Mean distance from center point to tree (min 12.5cm)}^2}$$

In order to determine the influence of forest density on sleep site and nest site selection, a comparative set of 'control' point density measures, unrelated to mouse lemur sleeping and nesting sites, were collected in a grid formation extending from the forest edge to the forest interior in the southern portion of S9 (**Fig. 25**). The grid consisted of five parallel lines of 250m, spaced at 50m intervals. PCQ measurements were recorded every 25m along each transect (from 0m to 250m). The grid was situated within the study area and overlapped with a number of known mouse lemur territories (see **Chapter 4**). Using a random number generator, 50 sleep sites and 50 forest density measurements obtained from the grid were used for comparison, along with all known leaf nest site densities, in order to assess whether local forest density is a factor in determining the selection of sleep and nesting sites. In this analysis, nest sites are distinguished from other sleeping sites, as they provide additional utility (Kappeler, 1998; Thorén et al, 2010) and their location may therefore be subject to different selection criteria.

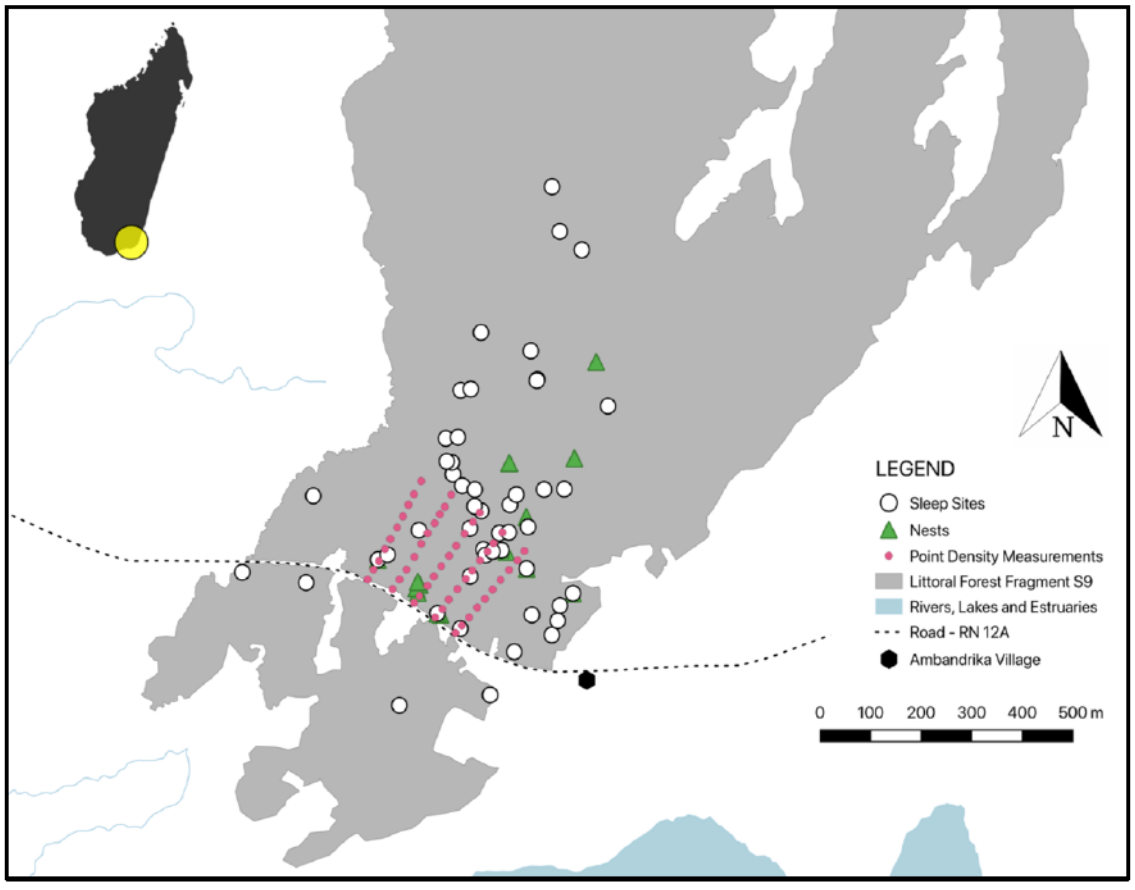

Figure 25 – The distribution of the 50 *M. tanosi* sleep sites, the location of each leaf nest observed in the study and the 50 control point density measurements used in the following statistical analysis.

Sleep site reuse and cohort stability was inferred by assessing the frequency that particular sleeping sites were reused, and how often individuals were observed sharing a site with familiar groups (Weidt et al, 2004; Karanewsky and Wright, 2015; Hending et al, 2018). Environmental data was used to determine whether site selection was influenced by weather condition. Although climate data was collected continuously throughout the study periods, only data relevant to each sleeping or nesting observation was used. The average temperature over the 24-hour period prior to sleep site selection (assumed to be at between 05.00 - 06.00am in the morning on the day of data collection) was tested for correlation against sleep site selection in each case where the lemur was directly observed, along with both the minimum and maximum values over the same period. Similarly, the average temperature over the previous 12-hour period of activity was tested (between 18.00pm - 06.00am), along with the average relative humidity over the previous window of activity. It was assumed that mouse lemurs will not change sleeping site during the day due to the risk of predation.

Data analysis was conducted using IBM SPSS version 26 (Chicago, IL, U.S.A). Chi-square tests were used to determine any baseline differences in the frequency of sleeping sites used, and to test for sex specific site preferences. Differences in the local forest density of selected sleep sites, nest sites and control forest point density measurements were assessed using Independent-Samples Kruskal-Wallis tests, with pairwise significance values adjusted by the Bonferroni correction for multiple tests. Comparisons between the tree height and DBH of sleeping sites and data obtained from forest point density PCQ data was assessed using Independent-samples Mann-Whitney U tests, as were comparisons between the sleep sites of male and female individuals. All microhabitat variables were checked for multicollinearity to eliminate redundancy and a Principal Component Analysis (PCA) was conducted to reduce the number of variables and produce a number of composite factors. A Generalized Linear Mixed Model (GLMM) was used to test for any significant difference in overall sleeping site microhabitat characteristics between sexes. In each model, sex was specified as a fixed factor, and sleeping site type and the average temperature over the previous 24 hours were set as covariates. Microhabitat characteristics (based on PCA output) were set as dependent variables and individual level data was incorporated as a random factor. Mann-Whitney U analysis was employed to test for differences in sleeping site reuse and site sharing percentages between sexes. Correlations between environmental conditions and sleep site selection were tested using Pearson's correlation, with positive associations tested using ANOVA. Significance level was set at $p<0.05$. Finally, binomial logistic regression analysis was conducted using a GLMM to test and predict which variables (microhabitat, environmental, biological) best account for the differences in sleeping site type selection, sleeping site reuse and

in multiple occupancy or sleep site sharing. In the case of sleeping site type selection, foliage sites were contrasted with tree holes, with nests excluded as they differ in terms of their specific utility.

Results

A total of 152 sleep and nest sites were visited during this study (59 for males, 93 for females). On 92 occasions the lemur was observed directly, and precise sleep and nest site details were recorded. On 60 occasions the mouse lemur was not observed directly although it was evident that the animal was in very close proximity. An overview of the general types of sleeping site used by *M. tanosi* in Sainte Luce is provided in **Table 18**. *Microcebus tanosi* preferentially opted to sleep in foliage sleeping sites with combined observations (tree canopy, *Pandanus* leaf axils, leaf nests or other foliage infrastructure sites) accounting for 90.13% and tree holes just 9.87% of all observed cases (X^2 DF=4; n=152; 125.89; p=<0.001). No significant difference was observed in the specific sleeping site types between sexes (X^2 DF=4; n=152; 4.87; p=0.301) or between foliage sites vs tree holes (X^2 DF=2; n=152; 0.42; p=0.811). *Microcebus tanosi* was observed using a total of 36 different tree and plant species as sleeping sites or for the structure of their leaf nests in Sainte Luce (**Table 19** and **Fig. 26**), with *Pandanus dauphinensis* used most often, accounting for 45% of all confirmed observations.

Table 18.

A summary of all sleep and nest observations in the study. Whilst values in the 'Lemur seen' group are accurate and derived from direct observations, values in the 'Lemur not seen' group are best approximations based on field notes made in close proximity to the lemur, but which remained concealed.

Observation Type		Sleeping Site Type				
		Tree Hole	Pandanus	Tree Canopy	Leaf Nest	Other
Lemur seen	Count (n=92)	12	49	22	6	3
	Percent	13.05%	53.26%	23.91%	6.52%	3.26%
	Males (n=40)	15.00%	40.00%	37.50%	2.50%	5.00%
	Females (n=52)	11.54%	63.46%	13.46%	9.62%	1.92%
Lemur not seen	Count (n=60)	3	14	42	1	0
	Percent	5.00%	23.33%	70.00%	1.67%	0.00%
	Males (n=19)	5.26%	15.79%	73.68%	5.26%	0.00%
	Females (n=41)	4.88%	26.83%	68.29%	0.00%	0.00%
Total	Count (n=152)	15	63	64	7	3
	Percent	9.87%	41.45%	42.11%	4.61%	1.97%
	Males (n=59)	11.86%	32.20%	49.15%	3.39%	3.39%
	Females (n=93)	8.60%	47.31%	37.63%	5.38%	1.08%

Figure 26 – *Microcebus tanosi* sleep sites in the littoral forests of Sainte Luce. **A**) Adult female emerging from leaf nest. **B**) Adult female concealed in foliage. **C**) A pair of adult females at a foliage sleep site. **D**) Five adult males huddled in open foliage. **E**) Adult female in *Pandanus dauphinensis*. **F**) A group of five individuals (three pictured) in *Pandanus concretus*. **G**) Three female mouse lemurs in *Pandanus dauphinensis*. **H**) A pair of female in *Pandanus dauphinensis*. **I+J**) Adult male concealed in a small tree hole. **K**) A group of four female mouse lemurs in a tree-split (*Dracaena reflexa var. nervosa*). **L**) Adult male in a tree hole at ground level. **M**) Adult male at the entrance to a tree hole. **N**) Adult male poorly concealed in a tree hole. **O+P**) An adult male and female concealed inside fallen *P. dauphinensis* leaves.

Table 19.

Tree species used as sleeping and nesting sites by *Microcebus tanosi* in the littoral forests of Sainte Luce between 18/08/2017 and 08/11/18 and their relative usage counts.

Species	Vernacular Name	Family	Count
Tambourissa purpurea	Ambora	Monimiaceae	1
Erica sparsa var. *sparsa*	Anjavidy	Ericaceae	1
Mammea sessiliflora	Ditsaky	Clusiaceae	2
Dracaena reflexa var. *angustifolia*	Falinandro	Conavallariaceae	5
Erythroxylum nitidulum	Fangora	Erythroxylaceae	1
Asteropeia sp.	Fanola	Theaceae	1
Asteropeia multiflora	Fanolafotsy	Theaceae	1
Plectronia densiflora	Fantiskahitry	Rubiaceae	4
Leptolaena delphinensis	Fonto	Sarcolaenaceae	3
Schizolaena elongata	Fotondahy	Sarcolaenaceae	1
Asplenium sp.	Hahabe	Aspleniaceae	1
Podocarpus madagascariensis var. *procerus*	Harambilo	Podocarpaceae	1
Cassine micrantha	Haramboanja	Celastraceae	1
Intsia bijuga	Harandrato	Fabaceae	1
Psorospermum sp.	Harongopanihy	Clusiaceae	1
Ludia sp.	Hazofotsy	Flacourtiaceae	1
Diospyros gracilipes	Hazomainty	Ebenaceae	6
Scolopia erythrocarpa	Lampivahatsy	Salicaceae	2
Anthocleista longifolia	Lindemlahy	Loganiaceae	1
Cynometra cloiselii	Mapay	Fabaceae	2
Erythroxylon sp.	Menahy	Erythroxylaceae	2
Pandanus concretus	Pandanus concretus	Pandanaceae	4
Pandanus dauphinensis	Pandanus Vakoa	Pandanaceae	59
Turraea lanceolata	Pimakarova	Meliaceae	1
Ravenala madagascariensis	Ravanala	Strelitziaceae	3
Eugenia sp.	Ropoaky	Myrtaceae	2
Syzygium emirnense	Rotry	Myrtaceae	9
Tina thouarsiana	Sanira	Sapindaceae	2
Malleastrum mandenense	Sarigiavy	Meliaceae	1
Tabanaemontana sp.	Sarivotaky	Apocynaceae	1
Phylloxylon xylophylloides	Sotro	Fabaceae	1
Sarcolaena multiflora	Vondroza	Sarcolaenaceae	4
Polyscias aculeata	Vontsila	Araliaceae	1
Grisollea sp.	Zambo	Icacinaceae	1
Noronhia ovalifolia	Zorafotsy	Oleaceae	1
Scolopia orientalis	Zoramena	Flacourtiaceae	2

Ecological drivers of sleeping site selection

Statistical comparison revealed a significant difference between the specific point densities of mouse lemur sleep sites, nest sites and control forest density points (F=6.443, df=2, p=0.040, n=115). Post-hoc results indicate a significant difference between the densities of selected sleep sites and control forest points (p=0.037, n=100), with sleeping sites being located in denser areas of forest. However, no significance was found between sleep site and nest site (p=1.000, n=65) or between nest site and the control forest points (p=0.619, n=65). Median point density values for each treatment group were as follows; 0.010 (1.0 trees/m^2) at observed sleep sites, 0.009 (0.9 trees/m^2) at observed leaf nests and 0.007 (0.7 trees/m^2) at control points. Microhabitat density recorded at each of the sleeping and nest sites ranged from 0.21 to 4.83 trees/m^2. No significant difference was found between the DBH of the sleep site trees compared against the control points (U=1251.500; p=0.992; n=100), or between the height of the sleep tree and the control points (U=1521.000; p=0.062; n=100), although a trend was noted.

A summary of the microhabitat characteristics of sleeping sites is presented in **Tables 20** and **21**, along with statistical analysis comparing sites used by both sexes (GLMM output). GLMM's ran for each variable independently revealed no statistically significant difference in the microhabitats of sleeping sites between the sexes across the seven variables. Principal Component Analysis (PCA) condensed the number of microhabitat variables from seven into two main factors, accounting for 65% of the cumulative variation combined (**Fig. 27**). Factor 1 comprised predominantly of characteristics relating to tree structure and size (tree height, DBH, crown width and sleep site height) and the factor 2 characteristics more closely related to canopy (sleep site - canopy distance and canopy cover).

GLMM analysis using both composite factors revealed a significant difference between sexes for Factor 1 (F=5.433; DF=1; p=0.023), with females selecting sites with higher Factor 1 values. The association between sex and sleeping site type also produced a near significant result (F=2.728; DF=3; p=0.052), with females appearing more likely to select tree holes in larger trees than males. In contrast, no significant difference was observed between sexes based on Factor 2. Similarly, no further significance was found in any of the additional covariates tested (sleep site type or climate variables) for either Factor, or in the interactions between variables. For both factors, the effect of individual variation was non-significant (Factor 1 Z=1.330; SE=0.044; p=0.184; Factor 2 Z=0.673; SE=0.095; p=0.501). Climate variables (temp and RH) showed considerable multi-collinearity and no significant interaction was found between these and sleeping site type.

Table 20.

Microhabitat descriptives. Median and range values for eight (four male, four female) individual mouse lemurs in Sainte Luce. Nest types refer to **Table 16**.

Sleep Site Character	ML 1 (M n=14)	ML 2 (M n=6)	ML 3 (M n=11)	ML 4 (M n=12)	ML 5 (F n=15)	ML 6 (F n=12)	ML 7 (F n=8)	ML 8 (F n=11)
Microhabitat density (trees/m2)	0.54 (0.21 - 1.23)	1.02 (0.78 - 1.25)	1.50 (0.90 - 3.00)	1.33 (0.76 - 2.72)	1.70 (0.69 - 4.83)	1.55 (0.80 - 4.70)	1.06 (0.57 - 1.84)	1.20 (0.80 - 2.80)
DBH (mm)	43.29 (12.73 - 73.21)	113.39 (81.81 - 522.03)	66.85 (39.79 - 149.61)	102.18 (36.29 - 145.79)	127.32 (54.11 - 522.03)	164.88 (101.86 - 177.30)	7.80 (94.86 - 138.15)	105.04 (54.75 - 146.74)
Lemur Height (m)	2.10 (0.5 - 4.5)	7.75 (4.0 - 15.5)	5.00 (0.65 - 8.0)	3.00 (0.25 - 6.0)	3.50 (0.4 - 10.0)	6.75 (2.0 - 8.0)	2.75 (1.6 - 5.2)	1.75 (0.5 - 7.0)
Tree Height (m)	3.50 (2.0 - 5.0)	10.00 (3.6 - 16.5)	6.00 (1.8 - 12.0)	6.30 (3.5 - 8.0)	5.50 (2.0 - 15.0)	7.80 (3.2 - 9.0)	4.80 (1.8 - 7.0)	4.90 (0.6 - 8.0)
Lemur - Canopy Distance (m)	0.50 (0.0 - 3.9)	2.10 (1.0 - 5.0)	2.00 (0.0 - 5.0)	2.75 (0.5 - 5.75)	1.80 (1.5 - 8.0)	1.35 (0.0 - 3.0)	1.90 (0.0 - 2.5)	1.20 0.0 - 5.5)
Crown Width (m)	1.60 (0.6 - 2.6)	5.00 (4.5 - 6.0)	1.60 (1.0 - 4.8)	2.90 (0.8 - 6.0)	3.50 (1.5 - 7.0)	3.30 (2.0 - 4.0)	2.90 (2.0 - 4.0)	3.20 (1.8 - 4.2)
Canopy Cover (%)	60.00 (20 - 100)	70.00 (10 - 80)	80.00 (50 - 100)	75.00 (40 - 100)	70.00 (30 - 100)	70.00 (20 - 70)	80.00 (60 - 80)	65.00 (40 - 80)
Nest Types (n)	2.00	4.00	4.00	4.00	3.00	2.00	2.00	4.00

Table 21.

Statistical description of seven sleeping site microhabitat characteristics for all study animals in Sainte Luce. GLMM analysis indicating differences in microhabitat characteristics between sex, with individual differences set as a random factor.

	Microhabitat density (trees/m2)	DBH (mm)	Lemur Height (m)	Tree Height (m)	Lemur - Canopy Distance (m)	Crown Width (m)	Canopy Cover (%)
Between Sexes							
Median male (n=33)	1.15	56.66	2.15	5.00	5.00	1.80	75.00
Median female (n=51)	1.10	111.72	3.50	6.50	5.50	3.00	74.00
Min-Max male	(0.2 - 3.0)	(12.73 - 522.03)	(0.2 - 15.5)	(1.8 - 16.5)	(0.5 - 12.5)	(0.5 - 6.5)	(13 - 100)
Min-Max female	(0.3 - 4.8)	(7.96 - 522.03)	(0.4 - 10.0)	(0.6 - 15)	(0.25 - 12.0)	(0.8 - 7.0)	(21 - 98)
GLMM							
Fixed Effect	F=0.110; p=0.741	F=1.536; p=0.219	F=0.096; p=0.757	F=0.328; p=0.569	F=0.390; p=0.534	F=2.250; p=0.138	F=0.042; p=0.838
Fixed Coefficient (Sex)	B=-0.07; SE=0.21	B=-0.33; SE=0.26	B=-0.06; SE=0.19	B=-0.08; SE=0.15	B=0.13; SE=0.21	B=-0.25; SE=0.16	B=-0.13; SE=0.06
Random Effect	Z=1.69; p=0.091	Z=1.99; p=0.046	Z=0.87; p=0.386	Z=1.22; 0.221	Z=1.55; p=0.122	Z=1.62; p=0.105	Z=0.58; p=0.563

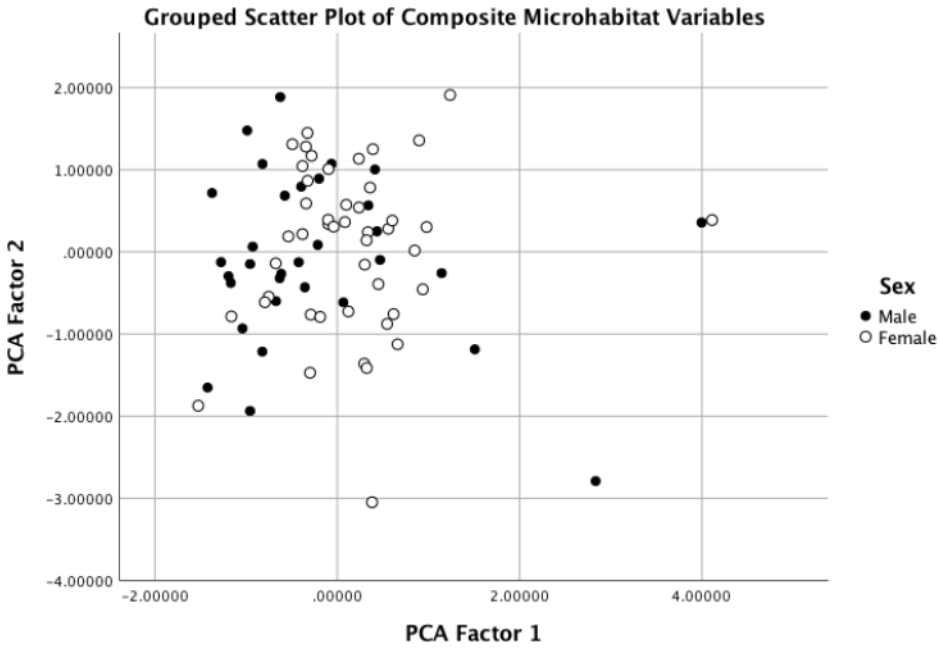

Figure 27 – A projection of the two main PCA composite factors, accounting for 65% of total variation across the seven microhabitat characteristics (sleeping site height, tree height, sleeping site and canopy distance, canopy cover, forest density and DBH). Factor 1 comprises mainly of tree height, DBH, crown width and lemur height, whilst Factor 2 comprises primarily of sleeping site to canopy distance and canopy cover.

Sociality and re-use of sleeping sites

Results show a statistically significant difference in cohort size at sleeping sites between sexes (U=475.500; p=0.022; n=54). The median number of additional lemurs, besides from the focal animal, observed at the sleep sites of male individuals is zero, and one in the case of females. However, the maximum number of individuals confirmed sharing with a focal male individuals was four, and three for the focal female. Individuals from both sexes were observed sleeping alone on multiple occasions (males in 73.9% of observations and females in 37.5% of cases). Comparison of individual lemur sleeping cohort size similarly produced a significant result (KW=34.990; df=19; p=0.014; n=53). Analysis of sleeping group composition, at least in terms of sex, was precluded as in the majority of cases, as cohabiting lemurs could not always be sexed accurately.

Of the 152 sleep sites recorded in the study, on only 14 occasions was a specific site used multiple times (representing 9.2% of all observations). Female individuals were observed to significantly

re-use sleep sites more regularly than males (U=3113.500; p=0.037; n=152). With all data pooled, females reused sleep sites in 12% of cases (n=93), in comparison to males who were only observed to reuse sites 5% of the time (n=59). In many instances, the lemur cohort within a sleeping site could not be determined accurately as occupants were not fully visible (n=37 or 40%), but on 55 separate occasions (60%) nest cohort could be clearly observed. On 29 occasions the focal lemur was observed to be alone (52.7%) whilst on 26 occasions, the focal animal was observed with others (**Table 22**). On just three occasions were two collared individuals observed co-habiting; two adult females were observed sharing a leaf nest, an adult male and an adult female were observed together in a tree hole and a pair of adult males were observed together in the leaf axils of a *P. dauphinensis* screwpine.

Table 22.

A breakdown of *M. tanosi* sleeping cohorts in Sainte Luce. Values represent minimum sleeping group size, as additional individuals may have remained out of sight in some cases.

Sex	**Sleeping Cohorts**					
	Unknown	Alone	Focal+1	Focal+2	Focal+3	Focal+4
Male (n=40)	17	16	4	2	0	1
Female (n=52)	20	13	12	3	4	0
Total (n=92)	37	29	16	5	4	1

Sleeping site type predictors

Non-parametric analysis (Pearson correlation) of climate data found no significant association between the type of sleep site selected and the average temperature recorded over the previous 24-hour period, or with any of the other highly correlated climate related variables (**Figure 28**). GLMM analysis using binary logistic regression was able to predict sleeping site, between foliage sites and tree holes with an accuracy of 89.6% (n=67). However, none of the eight predictor variables (five climate variables, sex and two condensed microhabitat characteristics) alone produced significant results (**Table 23**). In the predictive model, only PCA Factor 2 produced a trend towards significance (F=3.436; DF=1; p=0.069). Prediction of tree hole utilisation (correctly determining only 12.5% of cases) from the foliage sleeping sites (100% of cases) was poor despite the overall model accuracy. The same set of variables was able to predict multiple occupancy at sleeping sites with an accuracy of 97.7% (n=44; solitary cases=96%; site

sharing=100%). Again, none of the individual predictor variables produced a significant result, suggesting that a combination, or multivariate model is necessary. Finally, again using the same eight predictive variables, the model was able to determine sleeping site reuse with an overall accuracy of 87.5% (n=72; single use sites=72.7%; reuse=27.3%). Again, no single predictor variable was significant, although sex produced a trend towards significance (F=3.683; DF=1; p=0.060).

Table 23.

A summary of the output produced for each predictive variable in the GLMM binary logistic regression analysis. The high accuracy of each of the three models (Foliage sleeping sites vs tree holes, solitary site use vs multiple occupancy and single use vs multiple use) is evidently dependent on multivariate factors, with no single variables producing significant results.

Model	Variable	Output			
		F	DF	DF2	Sig.
Foliage vs Tree Holes	Microhabitat Factor 1	0.002	1	58	0.968
(Total model accuracy = 89.6%)	Microhabitat Factor 2	3.436	1	58	0.069
	Sex	0.299	1	58	0.587
	Avg Temp (24hrs)	1.000	1	58	0.321
	Avg Temp (12hrs)	0.175	1	58	0.677
	Max Temp Active	2.704	1	58	0.106
	Min Temp Active	0.772	1	58	0.383
	Avg RH (12hrs)	0.292	1	58	0.591
Solitary vs Multiple occupancy	Microhabitat Factor 1	2.776	1	35	0.105
(Total model accuracy = 97.7%)	Microhabitat Factor 2	0.356	1	35	0.555
	Sex	0.010	1	35	0.919
	Avg Temp (24hrs)	0.003	1	35	0.958
	Avg Temp (12hrs)	0.462	1	35	0.501
	Max Temp Active	0.007	1	35	0.935
	Min Temp Active	0.008	1	35	0.930
	Avg RH (12hrs)	0.282	1	35	0.599
Single use vs Multiple use	Microhabitat Factor 1	2.228	1	63	0.141
(Total model accuracy = 87.5%)	Microhabitat Factor 2	0.365	1	63	0.548
	Sex	3.683	1	63	0.060
	Avg Temp (24hrs)	0.148	1	63	0.702
	Avg Temp (12hrs)	1.629	1	63	0.206
	Max Temp Active	1.223	1	63	0.273
	Min Temp Active	0.247	1	63	0.621
	Avg RH (12hrs)	1.645	1	63	0.204

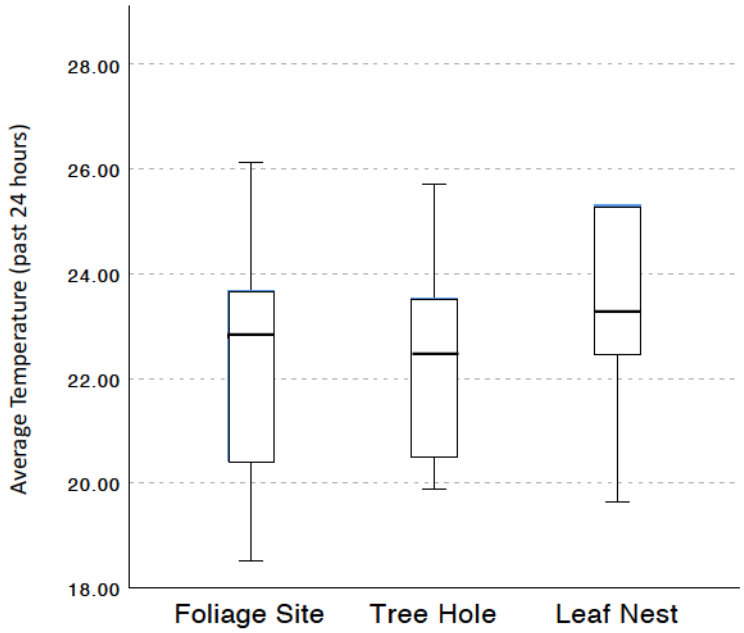

Figure 28 – Boxplot depicting the average temperature (horizontal lines) over the previous 24hour period prior to sleep site selection by *M. tanosi* in the littoral forests of Sainte Luce. Sleeping sites are amalgamated into three general categories. *Pandanus* sites are included within 'Foliage Sites'.

Discussion

The results of this study confirm *M. tanosi* as a habitat generalist, able to utilise a variety of sleeping site types and a wide range of tree species in the littoral forests. The species shows a clear preference for foliage sleep sites over tree holes, indicating that at least in the austral summer months, thermoregulatory considerations may be secondary to other factors. It appears instead that sleep site selection is determined to a greater extent by predator avoidance and social behaviours (particularly those linked to reproduction), at this time of year when average daily temperatures are higher (Jury, 2003; Vincelette et al, 2007c). The clear preference for foliage sleep sites is comparable with findings for other mouse lemur species e.g. *M. berthae* (79%), *M. griseorufus* (93%), *M. lehilahytsara* (100% although ex-situ) *M. rufus* (83.2%) and *M. sambiranensis* (93%) (Schwab, 2000; Génin, 2010; Jürges, 2013; Karanewsky and Wright, 2015; Hending et al, 2017), but contrast with findings for *M. murinus* who principally select tree holes (86%) and *M. ravelobensis* and *M. ganzhorni* who appear to equally use both tree holes and foliage sites (Radespiel et al, 2003b; Lahann, 2008). Whilst the limited use of tree holes may be simply a reflection of the limited necessity for thermoregulatory behaviour during the study

period, it may alternatively be a consequence of restricted resource availability, as has been postulated for *M. ravelobensis* at other forest sites (Radespiel et al, 2003b; Thoren et al, 2010). In Sainte Luce, this may be as a result of competition with the larger sympatric species *Cheirogaleus thomasi*, which almost exclusively uses tree holes (Fietz, 1999; Lahann, 2008). Such competition has been invoked in other forests in Madagascar for the seemingly reduced levels of tree hole utilisation by *Microcebus* species (Seiler et al, 2013). In contrast, there is currently no evidence to suggest any competition with *Cheirogaleus thomasi* for foliage sites in the littoral forests.

It is further evident from this study that Pandanaceae species, and particularly *Pandanus dauphinensis*, provide an important sleeping site resource. Results from a botanical assessment of Sainte Luce (S. Hyde Roberts, unpub. data) indicate that *Pandanus dauphinensis* is a very common species in Sainte Luce, existing at a density of roughly 66 plants per hectare in study fragment S9. Based on these estimates, there are over 20,000 *P. dauphinensis* plants in the study fragment alone. It is therefore unlikely that the number of available sleep sites is a limiting factor for population size and or growth. *Pandanus dauphinensis* are distributed throughout the intact areas of littoral forest, although appear to be less abundant at or near to the forest edge. *Pandanus acanthostylus* has also been reported as being an important sleep site species for *M. rufus* in Ranomafana NP (Karanewsky and Wright, 2015) and *P. baptistii* and other *Pandanus* species appear to be hugely important resources for ex-situ *M. lehilahytsara*, accounting for 86% of observed sleep site observations (Jürges et al, 2013). Thus, the Pandanaceae family may provide an important role in mouse lemur ecology in forests across Madagascar. A further study of the habitat utilisation of *M. ganzhorni* in Mandena (previously referred to as *M. murinus* prior to its taxonomic promotion) also noted the use of *Pandanus* screwpines (presumably *P. dauphinensis*), although to a much lesser extent than *M. tanosi* do in Sainte Luce. Lahann (2008) observed 18% of females and just 6% of male mouse lemurs in Mandena used the species (12% of total sleep site observations). In contrast, 47% and 32% of females and males respectively utilise the species in Sainte Luce. Such contrast in the relative use of different sleep sites between sexes is further echoed in the proportions of each sex observed using tree holes.

Although renowned for general degradation and high levels of resource extraction, the forest fragments of Sainte Luce are considered more intact than those in nearby Mandena (Lowry and Faber-Langendoen, 1991; Temple et al, 2012). In Mandena, *M. ganzhorni* utilises tree holes to a much greater extent (>46% of all cases) than *M. tanosi* in Sainte Luce, with females exploiting these microhabitats extensively (78% of all cases, compared to just 15% of males) (Lahann, 2008). In Sainte Luce, the proportion of females using tree holes is just 9%, and 12% in males. It

appears that female mouse lemurs in Sainte Luce instead opt to sleep in *Pandanus* screwpines. Furthermore, the forests of Mandena, although smaller, also support two con-generic species (*C. thomasi* and *C. major*) which rely almost entirely on tree holes for both sleep sites and for hibernation during the colder months. Competition for tree holes could be expected therefore to be more intense in Mandena than in Sainte Luce, where only a single species of *Cheirogaleus* (*C. thomasi*) occurs. However, dwarf lemur population density appears to be greater in Sainte Luce (Ganzhorn et al, 2008 and see **Chapter 6**) and could lead to intense inter-specific competition and a monopolization of high-quality tree holes by the larger lemurs. Both *M. ganzhorni* and *C. thomasi* are equally distributed within the littoral forests of Mandena (Lahann, 2008) and share a high degree of overlap in their diets, and there is no reason to suggest that a similar scenario does not hold true for Sainte Luce. It was also noted that on occasion, both *M. ganzhorni* and *C. thomasi* utilise tree holes in the same tree, although never in the same hole, implying that some competition exists between the two species. Niche theory predicts that sympatric species should develop differentiated adaptations in order to coexist (Pianka, 1981; Walter, 1991), and whilst *M. tanosi* and *C. thomasi* share many broad ecological characteristics, differences in sleep site utilisation might be a factor that ecologically discriminates the species (Radespiel et al, 2003b).

Pandanus dauphinensis provide a unique forest architecture, with broad radial crowns forming an axial base above the stem which acts as a reservoir and can collect water, dead leaves and other organic matter. This material provides ideal hiding spaces for mouse lemurs, particularly from aerial predators, whilst the size and orientation of the leaf axils enables multiple mouse lemurs to occupy a single plant (**Fig. 26 F+G**). Multiple occupancy at sleep sites has been demonstrated to enable individuals to better maintain body temperature through close contact, whilst also decreasing predation risk by means of increased vigilance and lessening the probability of individual predation if discovered (Alexander, 1974; Perret, 1998; Schmid, 1998; Radespiel et al, 2003b). Furthermore, the radial nature of the base of the crown permits a 360° escape route. *Pandanus dauphinensis* also has a number of defensive characteristics that could deter or limit access to some predatory species, such as a row of sharp prominent spines along the leading edges of leaves, as well as a row on the underside of the leaves, a high bole height, making access relatively difficult from below and long, unsupported leaves making lateral access difficult for larger bodied animals. However, a study of the usage of *P. dauphinensis* by the herpetofauna of Sainte Luce reported observations of two noteworthy mouse lemur predators (*Ithycyphus oursi* and *Sanzinia madagascariensis*) within the plant's axils (Lehtinen, 2002). The foraging behaviour of these two snakes is likely an important factor explaining why individual mouse lemurs appear to select a different sleep site each day i.e. it is an anti-predatory strategy. Whilst neither snake

species are particularly abundant in the community, *P. dauphinensis* density is high, and so selecting a different sleeping site on a daily basis may reduce the risk of detection and predation by arboreal snake predators, both of which hunt predominantly by means of olfaction.

In terms of specific microhabitat characteristics, the results of this study further reveal that individual *M. tanosi* select their sleep sites specifically in denser patches of forest than could be expected by chance, further indicating that predation risk is a key consideration. Mouse lemurs are reliant on their ability to avoid detection by predators, and by concealing themselves in denser patches of forest they are likely more difficult to detect by visual predators such as birds. There is no doubt that avian predators constitute a serious threat to mouse lemurs (Goodman et al, 1993), and a large number of candidate predator species exist in Sainte Luce (see **Chapter 2**, **Mouse lemur predators**). Given that most avian predators are silent, and there is no evidence for any means of olfactory detection in mouse lemurs (Kappel et al, 2011), vigilance, eavesdropping and the selection of cryptic diurnal shelters provide the best response (Seiler et al, 2013). Certain predators may also be less able to access the densest areas of forest, or at least approach without detection, again favouring the sheltering individual. Although the localities of nest sites could be expected to be even more carefully selected than sleep sites, given the importance of protecting neonates, nest sites did not differ significantly from either sleeping sites nor randomly selected points in the forest. However, this could possibly be an artefact of sample size, with fewer nest sites included in the analysis relative to the sleeping site data.

Whilst Lahann (2008) reported clearly demarcated and sex-specific sleep site selection in *M. ganzhorni*, this study found no evidence that male and female *M. tanosi* select different sleep site types. This finding appears to be in line with several other species studied to date (Radespiel et al, 1998; Hending et al, 2017), although not all studies report this comparison (Schwab, 2000; Génin, 2010; Jürges, 2013; Karanewsky and Wright, 2015). However, results reveal that females select sleeping sites with specific microhabitat characteristics that were differentiated from those of males. Given that females depend on sleeping sites for birthing and to raise and cache young, and in general have different reproductive strategies from males, this is perhaps no surprise (Trivers, 1972; Kappeler, 1998; Fietz and Dausmann, 2003; Eberle and Kappeler, 2006). Females were found to select sleeping sites in trees with a suite of size related characteristics i.e. taller trees with larger diameters and with broader crowns than male individuals. Other studies have reported similar sex-specificity in terms of microhabitat traits, with *M. murinus* females selecting tree holes higher in trees, with larger volumes and better insulative capacity (Radespiel et al, 1998), whilst *M. ganzhorni* females select both taller and larger diameter trees (Lahann, 2008).

Conversely no such sex-specific traits were detected in *M. sambiranensis* (Hending et al, 2017). Whilst the selection of trees with broader tree crowns may facilitate some protection from aerial predators, the selection of larger diameter trees is more difficult to explain given that females show no greater preference for tree holes than males. The selection of larger diameter trees could be a simple correlational artefact, but also may be a reflection of the increased social cohesion of female groups, with larger trees better able to support multiple individuals. Larger trees may also support richer invertebrate communities offering improved feeding benefits. Ultimately, these characteristics could also help to increase the security of neonates and infants (Kappeler, 1998) and may reflect differentiated parental investment between the sexes (Radespiel et al, 1998).

This study also found that individual *M. tanosi* change sleeping site very frequently and found no evidence to support concurrent sleeping site reuse, although consecutive daily observations were uncommon. The very low sleeping site fidelity (<10%) again supports the hypothesis that predator avoidance is a key consideration for mouse lemurs in Sainte Luce and indicates that predator pressure may be very high. Females were shown to reuse sleeping sites more often than males on average (12% vs 5%), likely a reflection of male reproductive strategy, with males exhibiting more extensive ranging behaviour in search of receptive females (see **Chapter 4**). In several species, but not all, male mouse lemurs occupy larger home ranges than females in the mating season (Dammhahn and Kappeler, 2005; Lahann, 2008; Hending et al, 2017). In pursuit of receptive females, it is perhaps no surprise that males reuse sleeping sites less frequently than females as they search wide areas (Trivers, 1972; Emlen and Oring, 1977; Clutton-Brock, 1989). Alternatively, reducing social contact and the risk from transmittable diseases and parasite burden may be a further means of maintaining male fitness (Altizer, 2006). The disparate pattern of sleep site reuse between sexes is similar to that observed in other mouse lemur species (e.g. *M. murinus*, *M. ganzhorni*, *M. griseorufus*) (Radespiel et al, 2003b; Lahann, 2008; Génin, 2010), but is most similar to *M. sambiranensis* (Hending et al, 2017), with both sexes exhibiting relatively low site fidelity. However, sleep site re-use in *M. tanosi* is very low compared with other known Cheirogaleid species (e.g. *M. murinus* 82%; *M. ravelobenisis* 38%; *M. griseorufus* 34%; *A. trichotis* 69%; *C. major* 100%) (Radespiel et al, 2003b; Lahann, 2008; Biebouw et al, 2009; Génin, 2010).

In contrast, the rate of sleep site sharing was found to be relatively high in this study, with 47% of focal lemurs observed to be sharing a sleeping site. Females were found to be more gregarious, and significantly more likely to cohabit sleeping sites and nests than males. Males individuals were found to mostly sleep alone (74% of observations), as in other studied species (e.g. *M.*

murinus 75% and *M. ganzhorni* 71%), but not all (e.g. *M. ravelobensis*) (Radespiel, 2003b; Lahann, 2008). The selection of sites with larger structural traits by females supports the theory that sites are selected on the basis of their capacity for sharing and indicates a strong tendency towards sociality. Site sharing is perhaps more of a critical consideration for females, particularly during the reproductive season, as both the conservation of energy and the acquisition of resources are key facets of female evolutionary and reproductive success (Trivers, 1972). Captive *M. murinus* have been demonstrated to reduce energetic consumption by up to 40% by sharing sleeping sites and utilising thermoregulatory behaviours such as huddling (Perret, 1998). Indeed, in the majority of cases where cohabiting lemurs were observed in this study, individuals were often seen in very close proximity, evidently engaged in thermoregulatory behaviour. In contrast, male individuals attempt to maximise their access to receptive females by means of 'scramble competition', and so are more likely to devote more time and energy to ranging behaviours, and as a result may often sleep alone or in unstable groupings or in high-risk locations (Wells, 1977; Schwagmeyer, 1988; Kappeler, 1997b; Radespiel, 2000; Kraus et al, 2008). Whilst accurately determining sleeping cohorts was beyond the means of this study, the difference in the sharing patterns of individual lemurs suggests that sleeping cohorts are largely unstable and fluctuate frequently. Observations made during this study also highlight the highly variable sleeping configurations of *M. tanosi* in Sainte Luce. So, whilst sleep site sharing patterns are likely driven by a complex interaction of social factors (e.g. familial relationships, reproductive strategies, dominance hierarchies), predator avoidance, thermoregulatory requirements and resource availability (forest condition and competition), they are also underpinned by the fundamental biological constraints of sex.

A crucial consideration when interpreting the broader context of these results and making comparisons between mouse lemur species is study seasonality. Of the now nine species studied to date, none have full year-round data (although some investigations are extensive e.g. Lahann, 2008; Génin, 2010), and many investigations are conducted over just a single season. As a result, clear patterns are difficult to fully discern. In order to properly assess the influence that thermal insulation has on the selection of sleeping sites and mouse lemur behaviour in the littoral forests of Sainte Luce, a comparative study would be needed during the colder austral winter. Although annual fluctuations in temperature are relatively modest in the littoral forests in comparison to other areas of Madagascar (Jury, 2003; Vincelette et al, 2007c), a result of oceanic buffering, cold temperatures during the winter period likely present a thermoregulatory challenge. At present it is unclear whether or not *M. tanosi* undertakes bouts of daily torpor during winter, but it is conceivable since such strategies are employed by other closely related and proximally distributed

species (Perret, 1988; Radespiel et al, 2003; Weidt et al, 2004; Atsalis, 2008). It is therefore possible that *M. tanosi* utilise tree holes more readily in the colder months, exploiting the thermal stability they provide (Schmid, 1998). Compellingly, a winter study of *M. rufus* demonstrated both serial and concurrent tree hole reuse at Ranomafana NP, concluding that thermoregulation was the principal reason for the sleeping site selection (Karanewsky and Wright). It is therefore possible that *M. tanosi* similarly employs differentiated seasonal strategies in the littoral forests.

In conclusion, this study finds that the behavioural ecology relating to sleep site selection by *M. tanosi* in the littoral forests of Sainte Luce is best explained by predator avoidance and social constraints governed by sex. The data collected appears to fit a specific scenario under which predator avoidance is a key factor, at least during the reproductive season (Radespiel, 2000; Atsalis, 2008). Individuals exhibit low sleeping site fidelity, frequently change site as to avoid detection, demonstrate high levels of sleep site sharing and select sites with defensive attributes. Whilst improving predator detection is recognised as a fundamental advantage of sociality in primates (Alexander, 1974; van Schaik, 1983; Terborgh and Janson, 1986), there are possibly few more defensive plants than *Pandanaceae* in Madagascar's forests. In contrast, the limited number of sleep site observations utilising tree holes indicates either a reduced demand for well insulated sites, or less plausibly, low site availability (Lahann, 2008). As both sexes frequently change sites, it is unlikely that individuals are selecting favoured high-quality sites with specific characteristics, which would be expected if high levels of competition existed. Furthermore, the distribution of sleeping sites includes many localities near to the forest edge and in relatively open and exposed locations, in areas of highly degraded forest likely to be highly thermally unstable. Combined, these traits indicate a reduced need for thermally optimal sleeping sites. However, during the winter period the priorities of *M. tanosi* individual may change and the importance of well insulated sites may take precedence over other factors. This study provides the first ecological data pertaining to the sleep and nesting ecology of *M. tanosi*, and the results may help to inform lemur conservation initiatives and littoral habitat restoration projects in the future. Whilst predator avoidance appears to predominantly govern mouse lemur behaviour during the austral summer, understanding the strategies employed by *M. tanosi* to cope with thermal stress year-round would provide great insight into the species capacity for survival as the climate is set to become more unpredictable (Ingram and Dawson, 2005; Tadross et al, 2008).

CHAPTER 6

Population dynamics of nocturnal lemurs in littoral forest fragments

Background

Our understanding of the primate fauna of Madagascar has developed rapidly over the past few decades, emphasising the extraordinary importance of the island as a global repository for biodiversity (Myers et al, 2000; Ganzhorn et al, 2001; Mittermeier et al, 2005; 2010). Approximately one-fifth (114) of the worlds 505 recognised primate species are endemic to the island (Estrada et al, 2017), and new species continue to be described on a regular basis (Hotaling et al, 2016; McLain et al, 2017; Schüßler et al, 2020). Today however, 98% of lemur species are classified as being threatened with extinction (either listed as Vulnerable, Endangered or Critically Endangered) by the International Union for Conservation of Nature (IUCN, 2020) and five are listed among the world's 25 most endangered primates (Schwitzer et al, 2017). Furthermore, 100 species are reported as experiencing population declines (Schwitzer et al, 2014). In order to properly understand lemur population dynamics, and how species are responding to intensifying anthropogenic threats such as habitat loss, degradation, habitat fragmentation and hunting, it is crucial to obtain reliable estimates of both population size and density (Ganzhorn and Schmid, 1998; Müller et al, 2000; Plumptre and Cox, 2006; Ganzhorn et al, 2008; Erhart and Overdorff, 2008; Quéméré et al, 2010).

Whilst the greatest threat to tropical biodiversity is evidently largescale deforestation and habitat loss (Sala et al, 2000; Runyan and D'Odorico, 2016; Estrada et al., 2017), the response of primate and lemur communities to anthropogenic disturbance and habitat fragmentation is complex (Marsh et al, 2013; Kamilar and Beaudrot, 2018; Gould et al, 2020). Lemurs are known to form highly nested assemblages, with both diversity and minimum viable population size seemingly correlated with forest patch size, habitat complexity, body mass and dietary regime (Ganzhorn et al, 1995; 2000; Lehman et al, 2006; Atsalis, 2008; Eppley et al, 2020). However, it is now becoming ever clearer that habitat fragmentation and the resulting isolation of populations generally imparts a strong negative effect (Gardner, 2009; Holmes et al, 2013; Knapp, 2013; de Almeida-Rocha et al, 2017; Eppley et al, 2020; Kling et al, 2020), even in ecologically adaptable species. However, for some species, and in the short-term at least, the effects are not always

adverse (Ganzhorn et al, 1997; Irwin et al, 2010; Herrera et al, 2011; Lehman et al, 2006; 2006b) and species-specific responses are extremely important, complicating generalised genus level assumptions (Balko and Underwood, 2005; Lehman et al, 2006; 2006b; Herrera et al, 2011; Malone et al, 2013; Andriatsitohaina et al, 2020; Steffens et al, 2020).

It is also well documented that many lemur species are able to tolerate and utilise anthropogenic biomes (Ganzhorn, 1991; Donati et al, 2016; Eppley et al, 2016; Miller et al, 2017; Knoop et al, 2018). Whilst there is evidently variation in how individual species respond to the effects of fragmentation and degradation (Oklander et al, 2010; Knapp, 2013; Steffens et al, 2020), even among close congeneric species (Ganzhorn et al, 2007; Wright et al, 2008; Herrera et al, 2011; Malone et al, 2013) there is little doubt that forest patch size is a fundamental determinant of population size and is therefore a vital consideration when assessing demographic trends and developing conservation initiatives (Kling et al, 2020). Given that Madagascar's forests have experienced largescale declines over the past century (Green and Sussman, 1990; Harper et al, 2007; McConnell and Kull, 2014), there is no doubting the importance of understanding both generalised and species-specific lemur responses to forest degradation (Marsh et al, 2013; Lehman et al, 2006; Andriatsitohaina et al, 2020; Eppley et al, 2020; Gould et al, 2020).

The littoral forest formations of eastern Madagascar represent one of the most threatened ecosystems on the island (Schatz, 2000; Schatz et al, 2002; Ganzhorn et al, 2001; QMM, 2001), with conservative estimates suggesting only 10% of original forest cover remains (Consiglio et al, 2006; Vincelette et al, 2007b; Temple et al, 2012). Furthermore, what little is left of this coastal forest is now severely fragmented, (Du Puy and Moat, 1996; Ratsirarson and Goodman, 1997; Ganzhorn et al, 2001) and continuity with lowland evergreen forests further inland is now almost entirely broken (de Gouvenain and Silander, 2003). In the extreme southeast, several important littoral forest stands remain (Du Puy and Moat, 1996), of which, those in Sainte Luce are considered to be the most intact (Lowry and Faber-Langdoen, 1991; Rabenantoandro, 2001; Bollen and Donati, 2006; Rabenantoandro et al, 2007; Vincelette et al, 2007b; Temple et al, 2012). Today, Sainte Luce supports four lemur species including three strictly nocturnal species; *Avahi meridionalis* (EN), *Cheirogaleus thomasi* (EN) and *Microcebus tanosi* (EN) (Donati et al, 2020b; 2020c; Ganzhorn et al, 2020), with each having been subject to major taxonomic reassessment within the past 15 years (Zaramody et al, 2006; Rasoloarison et al, 2013; Lei et al, 2014). *Eulemur collaris*, a cathemeral species, today occupies only a small number of forest fragments; its distribution likely the result of high historic hunting pressure and subsequent extirpation (Hyde Roberts et al, 2020). In contrast, *A. meridionalis*, a folivorous species (Norscia et al, 2012), and

the other two Cheirogaleids (*C. thomasi* and *M. tanosi*), both considered generalist omnivores (Mittermeier et al, 2010), are more ubiquitous and have been observed in all remaining forest fragments in Sainte Luce surveyed to date. (see **Chapter 2**, **Study area**). At present, the nature and magnitude of the threats facing the nocturnal lemur populations are not well understood, although habitat destruction is considered a primary concern. In the past, hunting and bushmeat consumption has been prevalent in the area (Bollen and Donati, 2006), although it appears to have abated over the past decade (S. Hyde Roberts. pers. obs).

Due to past and present habitat destruction, it has been predicted that the majority of remaining littoral forest fragments are now too small to sustain viable populations of forest dependent species such as lemurs long-term (Cowlishaw, 1999; Ganzhorn et al, 2000). It is estimated that forest fragments of around 1000ha are required to sustain fully diverse vertebrate communities (Ganzhorn et al, 2000), indicating that conservation and reforestation initiatives are urgently required, with large bodied species most at risk of extirpation from smaller fragments. However, this suggested threshold far exceeds the majority of remaining forest habitats in Madagascar (Harper et al, 2007), and has provoked debate about the feasibility of conservation in fragments (Harcourt and Doherty, 2005; Gibbons and Harcourt, 2009). Whilst there is now evidence that *E. collaris* can traverse between isolated fragments up to distances of 1.5km on rare occasions (Donati et al, 2007; Bertoncini et al, 2017; Hyde Roberts et al, 2020), the separation between most forest patches is deemed insuperable for the strictly arboreal and nocturnal lemur species. In Sainte Luce, several protected forest fragments are currently separated by distances of well over a kilometre and in some cases by impassable aquatic systems (**Fig. 29**). Long-term monitoring studies are therefore critical to detect population level changes, especially among species with limited dispersal capacity, providing an early warning signal to conservationists and enabling the development of effective conservation strategies and the opportunity to effect interventions. Furthermore, the ecological roles that primates such as lemurs play in maintaining ecosystem health underscores the importance of their survival in threatened forests (e.g. Chapman, 1995; Chapman and Onderdonk, 1998; Levey et al, 2002; Bollen et al 2004; Lahann, 2007; McConkey et al, 2012; Chapman and Dunham, 2018; Ramananjato et al, 2020).

In addition to the effects of fragmentation, degradation and diminishing patch size, mining initiatives in the region (QMM, 2001; Vincelette, 2003; Rio Tinto QMM, 2010; Temple et al, 2012) provide an additional threat to existing forest cover and biodiversity (Schatz et al, 2000; Bollen and Donati, 2006; Watson et al, 2010; Hyde Roberts et al, 2019; Goodman et al, 2019). Under current proposals, mining operations are anticipated to remove an estimated 66% of

existing littoral forest cover in the southeast (Vincelette et al, 2007), including ca. 57% of forest cover in Sainte Luce (see **Chapter 2**; **Study area**), affecting forest habitat currently inhabited by lemurs. However, the mining project has financed and attracted much associated research and as a result there is now a significant body of literature focusing on Sainte Luce and littoral biodiversity (Lewis Environmental Consultants, 1992; 1992b; Andrianasolo et al, 2006; Bollen and Donati, 2006; Ganzhorn et al, 2008). In addition, the contextual history of the study area is very well documented (Ganzhorn et al, 2007; Virah-Sawmy et al, 2009; Temple et al, 2012). Furthermore, as of 2015, midway through the study, the management regime of a number of forest fragments in Sainte Luce was changed, with five (S1, S2, S8, S9 and S17) gaining official IUCN protected status, whilst two fragments (S6 and S7) were designated as community resource forests (**Fig. 5 + 29**). Whilst the effects of protected areas on wildlife communities and primates are far from clear (Beaudrot et al, 2016; Kamilar and Beaudrot, 2018), this change provided a further opportunity to assess the impact of local forest management policies on a well-studied lemur community, and to assess the time over which such measures may yield tangible impacts.

As a result, the littoral forests in the extreme southeast now represent a useful model to test community level responses to a range of key ecological parameters and conservation measures (e.g. patch size, forest management regime, species body mass, diet and habitat requirement), based on long-term monitoring and population dynamics. This study provides a first longitudinal assessment of the lemur communities in the littoral forests of Sainte Luce and offers insight into the mechanisms driving population dynamics. This study aims to provide a reliable assessment of the nocturnal lemur community in Sainte Luce and investigate the impact of fragment size and forest policy on population dynamics and long-term survival. The following hypotheses and predictions are tested:

1. If fragmentation and anthropogenic disturbance leads to an increasing scarcity of key lemur resources, it is predicted that all three nocturnal lemur species will show a declining population trend over time. Furthermore, if viable population size is correlated with forest fragment size, it can be further predicted that larger forest fragments will support larger and more stable lemur sub-populations.

2. If the functional traits and ecological requirements of a species (such as size, diet and niche) influence their vulnerability to decreasing fragment size and increasing habitat disturbance, it is predicted that: 1. *Microcebus tanosi* will be highly abundant in all study fragments, due to its small size, broad diet and fine branch niche. 2. *Avahi meridionalis* will show negative

population effects in both the smallest fragment and community use forest, because it is the largest and most conspicuous study species, with a preference for tall, large trees. 3. *Cheirogaleus thomasi* sub-populations will be negatively impacted by fragment size and habitat disturbance due to their need for resources vital to hibernation.

3. The designation of protected areas and community use forest fragments directly impacts lemur demographics as important resources are either safeguarded or harvested, with increasing effect over time. If this is the case, then it is predicted that the increased habitat degradation seen in the community forests since 2015 will have negatively impacted the local lemur community. In contrast, a positive population signal is predicted in the protected fragments over the same period as anthropogenic disturbance abates. It is further predicted that all three nocturnal species will exhibit similar responses to these management interventions.

Methodology

Sainte Luce (24°46'52"S; 47°10'28"E) lies within Madagascar's humid bioclimatic zone in the southeastern coastal lowlands, ca.45 km north of Tolagnaro/Fort Dauphin (the Anosy regional capital). These specialized humid evergreen woodlands are adapted to low altitude (0–50 m a.s.l), sandy coastal substrates and support high levels of diversity and endemism (Lowry and Faber-Langendoen, 1991; Lewis Environmental Consultants, 1992b). The area receives an average annual rainfall of ca. 2690 mm, with temperatures relatively constant with a mean annual temperature of 28°C (Goodman et al. 1997, Vincelette 2007c). Today, the littoral forests of Sainte Luce consist of a series of 17 disconnected forest fragments set amidst a matrix of ericoid grassland, swamp and sparse exotic tree plantations (Ingram and Dawson, 2006; Virah-Sawmy et al. 2009). Combined the remaining forest patches cover approximately 1,650ha, with fragments ranging in size from ca. 7ha to 368ha. This forest habitat type is recognised as a distinct phytogeographic unit (Ratsivalaka-Randriamanga, 1987; Lowry and Faber-Langendoen, 1991) and is often defined as a dense and humid lowland forest with a relatively open or non-continuous canopy (Bollen and Donati, 2006; Consiglio et al, 2006). Average canopy height ranges between 10-15m in Sainte Luce (Goodman, 1997) with emergent trees occasionally reaching 20m and over. The fragments are degraded to various extents, the result of decades, if not centuries of selective and non-selective resource extraction by dependent local communities.

In this study, a Distance sampling methodology was selected, with data collected using line transects, exact perpendicular distances and single observer configuration. Distance sampling is generally considered a key method for producing robust abundance and density estimates of wild plant and animal populations (Leopold, 1933; Struhsaker, 1981; Buckland et al, 2001; 2015) and has been widely employed in primatology for at least half a century (e.g. Southwick and Cadigan, 1972; Wilson and Wilson, 1975; Struhsaker, 1981; Plumptre and Reynolds, 1996; Brugiere et al, 2000; Nijman and Menken, 2005). Furthermore, line transect based distance sampling is widely used in the study of lemurs in Madagascar (Johnson and Overdorff, 1999; Radespiel et al, 2001; Lehman, 2006; Norscia, 2008; Ganzhorn et al, 2008; Quéméré et al, 2010; Meyler et al, 2012; Nguyen et al, 2013), although with some caveats (Müller et al, 2000; Radespiel et al, 2001).

Surveys were conducted between January 2011 and December 2018, across four forest fragments, running continuously throughout each year. Fragments S7, S8, S9 and S17 were selected for study as they constitute the largest and most accessible patches of littoral forest in Sainte Luce and support representative lemur assemblages. S17 was surveyed only to confirm the presence/absence of lemur species and was not included in the long-term monitoring protocol. Forest fragment naming convention follows QIT Madagascar Mineral's (QMM) standard designation (Lowry and Faber-Langdoen, 1991; Lewis Environmental Consultants, 1992). The fragments are relatively clustered and situated close to the major human settlements, and as a result, each has a differentiated extractive resource history. Together, the study fragments exhibit a variety of broad physical attributes (differing in extent, tree species composition, canopy height and canopy cover) that may influence lemur population dynamics. Transects within each fragment were selected along established forest routes to minimise disturbance. As a consequence, transects are not equal in length but instead vary in relation to the size and shape of the study fragment. A summary of relevant fragment and transect information is presented in **Table 24**. In total, 16 transect routes were established within the four study fragments, ranging in length from 220m (min) to 1,007m (max). With the exception of S17, all transects run perpendicular to the forest edge and are relatively evenly spaced (**Fig. 29**), guarding against the possibility of several lines being positioned by chance in areas of either high or low lemur density.

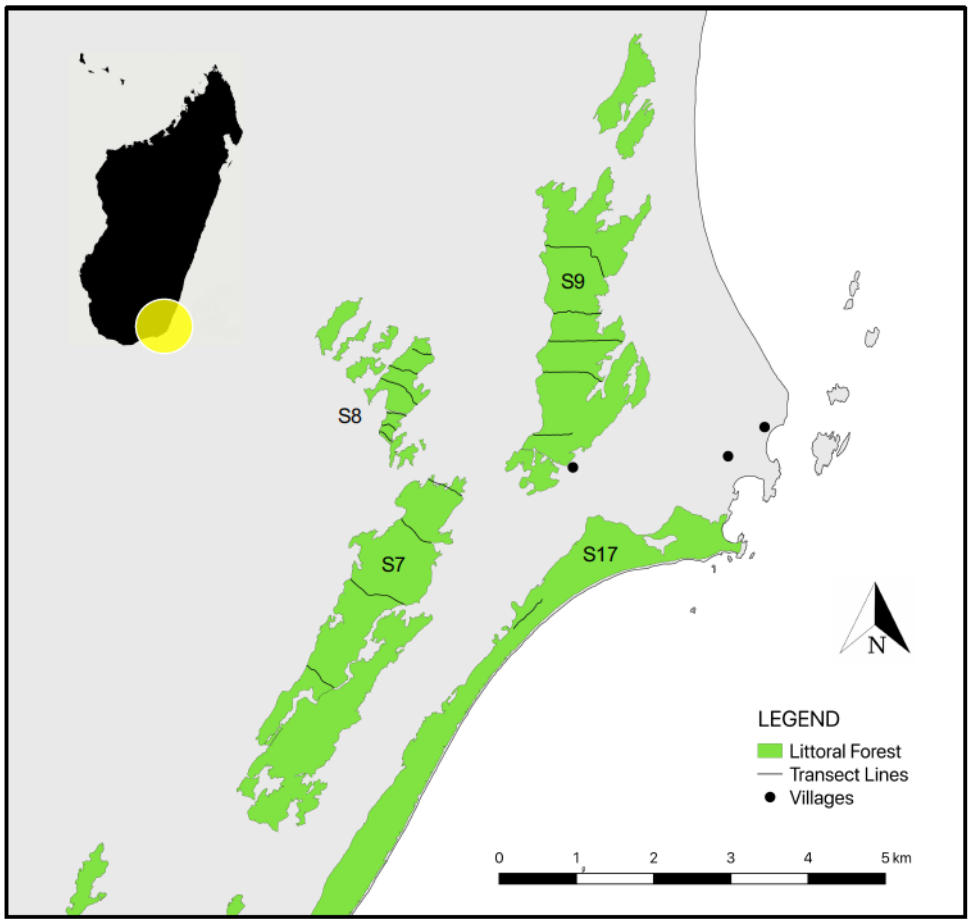

Figure 29 – The relative position and length of the 16 transects across the four study forest fragments (S7, S8, S9 and S17) (UTM 38J 719448 mE; 7257491 mS). Note that S17 has a single transect, established in order to ascertain and confirm the presence/absence of each species, and is not part of the regular monitoring schedule.

Surveys followed a standardised protocol, commencing between 18.00 – 19.30pm. A small research group (five researchers maximum) followed a pre-determined transect route, walking between 0.5-1km per hour, with speed set by trained local guides. Observer team composition changed continually over the course of the study. However, the continuous involvement of longstanding and fully trained local guides serves to minimize observer bias across years (Buckland et al, 2001). Torches were used to locate and identify lemurs at distance. Relative silence was maintained throughout the duration of the survey to prevent potential disturbance of animals ahead. The direction in which a transect was walked was regularly alternated as recommended by Buckland et al (2001). Although transect routes are pre-scheduled to ensure equal coverage throughout the year, some transects became inaccessible at certain times and in some weather conditions.

All forest levels were carefully scrutinised, based on the understanding that the lemurs in Sainte Luce exhibit some degree of separation based on height and forest strata (Lahann, 2008). During each survey, a single team member was responsible for recording data. Once an observation was made, a set of key parameters was recorded including GPS location, a unique dated GPS code, observation time, species, the sex of the animal if possible, and the exact perpendicular distance from the transect at the nearest position (measured to the nearest cm using a 50m tape). For *A. meridionalis*, a pair or family group living species, the number of observed individuals was noted along with group spread in metres. The estimated height of the animal from the ground and of the tree it was first observed in was estimated to the nearest meter, tree DBH was measured to the nearest millimetre, and the canopy cover directly above the initial lemur location was estimated as a percentage.

Descriptive population analysis was carried out using the software DISTANCE 7.3 and the CDS FORTRAN engine, based on the 'Buckland' line transect method (Thomas et al, 2010). The Cheirogaleid species, *C. thomasi* and *M. tanosi*, are considered solitary foragers and observations were treated as being independent. Conversely, observations of the Indriid, *A. meridionalis*, were treated as clusters. Adjustments were made to the underlying data in order to account for the hibernation period of *C. thomasi*, excluding transect data from the beginning of May to the end of September. Measurement units were recorded in metres (m) and hectares (ha) and no multipliers were set. Animal observations of +50m from the transect were excluded prior to analysis and considered as outliers (Buckland et al, 2001), often the result of animals being spotted across open areas and forest clearings, and even in separate forest remnants. In order to estimate population size, data were grouped into two-year sets to ensure sample size robustness, and each species was modelled independently for each of the three main forest fragments, and then globally (all fragments combined). All analytical model combinations were tested (i.e. model definitions or key functions combined with adjustment terms) and models were selected on the basis of Akaike Information Criterion (AIC) and Kolmogorov–Smirnov Goodness of Fit (GOF). Finally, models were fitted with varying truncation percentages in order to increase model accuracy and post-stratification techniques were applied to reduce sampling bias (Fewster et al, 2009). Where the number of observations falls below the recommended minimum required to accurately model detection function, set at 40 by Buckland et al. (2001), encounter rates were considered more useful (Ganzhorn et al, 2007).

Table 24.

General line transect characteristics, indictating the varying size of the forest fragments and transect lengths. Values in parentheses are standard deviations. Forest fragment size was established using GIS Tools (Google Earth Pro v.7.3.3 and CNES / Airbus 2020 imagery). Transect lengths were measured using a handheld Garmin GPSmap 62s device and Canopy Cover using a standard convex densiometer. Canopy heights are estimates made by a single researcher in an attempt to minimise error. Height and canopy cover were recorded at 10m intervals along each transect and averaged.

Fragment	Transect	Length (m)	Transect Repeats	Avg Canopy Height (m)	Max Canopy Height (m)	Avg Canopy Cover (%)
S7 (224ha)	T1	484	23	6.7 (3.5)	10	30.2 (17.6)
	T2	513	20	6.9 (3.8)	19	30.9 (17.0)
	T3	803	18	6.7 (3.6)	15	36.8 (24.5)
	T4	464	9	5.7 (4.6)	20	32.6 (26.3)
S8N (84ha)	T1	621	35	9.1 (5.9)	21	53.8 (31.5)
	T2	394	41	9.7 (5.1)	21	54.4 (30.2)
	T3	281	23	7.8 (4.1)	20	63.1 (31.3)
S8S (10ha)	T1	260	31	7.5 (4.9)	20	58.9 (32.2)
	T2	227	32	8.0 (5.6)	20	50.8 (28.5)
	T3	220	27	10.5 (5.9)	20	65.9 (33.9)
S9 (346ha)	T1	976	57	13.3 (7.3)	25	53.8 (29.6)
	T2	803	65	11.5 (6.3)	25	63.8 (29.8)
	T3	1007	28	9.6 (6.9)	24	51.4 (36.1)
	T4	516	55	8.4 (4.2)	20	59.4 (31.1)
	T5	660	20	13.8 (7.5)	24	62.3 (28.7)
S17 (359ha)	T1	572	3	11.9 (4.8)	20	71.2 (25.4)

Statistical analysis of the raw data (treated as year pairs for consistency with DISTANCE output) was undertaken using a Generalised Linear Mixed Model (GLMM) and conducted using the software in SPSS v.26. Species were tested both individually and grouped to provide a community overview. Models were fitted with a Poisson error distribution and log link function. Variables 'Year', 'Fragment' and 'Forest Protection' were treated as fixed effects, with the latter comparing the four-year periods both pre- and post-protected status change. Furthermore, the interaction between the two variables 'Year' and 'Fragment' was also incorporated into the model. The influence of transect placement was tested as a random effect. Finally, in order to account for the discrepancy in the number of transect repeats, the sampling effort was log transformed and integrated into the model as an offset variable (Barelli et al, 2015). Analysis of S8 (a fragment bisected by a road) showed no significant difference in the total number of lemur observations between north and south, or between the number of *A. meridionalis* and *M. tanosi* observations. As a result, the fragment is treated as a single patch in these instances. In contrast, a significant difference was detected in the number of *C. thomasi* observations, and the fragment was analysed as two separate areas. The level of statistical significance was set at 0.05.

Results

A total of 487 nocturnal transects were completed over the course of the study. A total of 285km of surveyed routes resulted in a total of 1,968 lemur observations (*A. meridionalis* n=1140; *C. thomasi* n=627; *M. tanosi* n=186). Each of the three nocturnal species were observed in all four study fragments.

Overall Population Estimates

The results of the population analysis (all study fragments combined) (**Table 25**) reveal a decline in the size of the *A. meridionalis* population between 2011 and 2014, falling sharply from an estimated 1281 individuals (LCI 793, UCI 2069) to 512 (LCI 325, UCI 806), a decline of 60.0%. Although rising slightly between 2015-2016, the downward trend appears to be continuing with the total population estimated at 480 individuals (LCI 348 – UCI 663) in 2017-2018. The vast majority of the *A. meridionalis* population in Sainte Luce resides within the largest fragment, S9, and the decline in this sub-population drives the overall trend (**Table 25** + **Fig. 30A**). In contrast, the sub-population in S7 is extremely small despite the relatively large size of the forest. Results from the smallest fragment S8 (north and south sections pooled), indicate the sub-population here is again small (<100 individuals), although appears relatively stable over the study period. Modelled sub-population estimates in both S8 and S9 show consistent trends, with both seeming to decline between 2011-2014 (by -53% and -45% respectively), before rebounding between 2014-2016 (by +73.3% and +23.0% respectively) and declining again through 2017-2018 (-11.5% and -30.4%). Similarly, the number of estimated *A. meridionalis* groups (N_s) tracked the general population estimates for both sub-populations in S8 and S9 (**Table 25**), whilst the mean number of individuals per group (E_s) declined overall from 1.73 individuals/group to 1.40 individuals/group over the study.

Global population estimates produced for *C. thomasi* reveal a minor decline in the overall number of individuals between 2011-2016, followed by a rapid population increase from an estimated 827 (LCI 639 – UCI 1069) to 1291 individuals (LCI 970 – UCI 1717) over 2017-2018. The species appears to be relatively abundant throughout all three study fragments, with the largest sub-population now occurring in S7 (**Table 25** + **Fig 30B**). Population estimates and linear trends suggest that whilst the sub-population in S9 is relatively stable, those in both S7 and S8 have shown a notable increase over the study period. Both sub-populations in S7 and S8 have expanded rapidly between 2016-2018, increasing from an estimated 296 to 490 and from 81 to 199 individuals, respectively. In contrast however, modelling population estimates for *M. tanosi* was

complicated by the low number of observations throughout the study. Results indicate that the *M. tanosi* population in Sainte Luce is very low but seems to have been relatively stable for most of the study (2011-2016), at around 200-280 individuals (**Table 25**). However, the overall population appears to have declined sharply over 2017-2018 (**Table 25** and **Fig. 30C**). The greatest proportion of the *Microcebus* population in this study appears to again inhabit the largest fragment S9, and this sub-population again largely determines the overall population trend. Estimates suggest a substantive global decline of 37% between 2015-2016 and 2017-2018. The number of direct mouse lemur observations made each year also shows a consistent decline.

Encounter Rates

Where the number of lemur observations is limited and the accuracy of the resulting population estimates is diminished, encounter rates offer an alternative measure of relative population density (Buckland et al, 2001). Encounter rates for *A. meridionalis* mirror the general population trend, highlighting the severe decline during the first half of the study, before fluctuating in subsequent year groupings (**Fig. 31D)**. **Figure 31A** reveals that *A. meridionalis* encounters have incrementally increased in S8 since 2013-2014, indicating possible population growth in the fragment. Encounter rate in S7 is extremely low. Over the course of the eight-year study, the species has been observed only three times in S7, with a single individual observed in 2013, a small family group (three individuals) observed in 2014 and a further singleton in April 2016, although several opportunistic sightings have also been made. Globally, *C. thomasi* shows a steady increase in encounter rate across the study period (**Fig. 31D**). A notable increase in encounter rate was observed in fragment S7, whilst the sub-populations in the other fragments appear stable but show no consistent trend **(Fig. 31B)**. Given the limited number of *M. tanosi* observations throughout the study, encounter rates provide a particularly useful metric. Encounter rate for *M. tanosi* is low (maximum 1.15 individual/km in S9 in 2015-2016) but relatively stable over the study (**Fig. 31D**). Notably, encounter rate shows an increase in S9 between 2011-2012 and 2015-2016 before dropping off (**Fig. 31C**).

Table 25.

Population descriptives for the three nocturnal lemur species across forest fragments S7, S8 and S9 combined between 2011 and 2018. Results based on pooled two-year datasets. The reduced effort attributed to *C. thomasi* is the result of excluded winter transects (May-Sept), when the species undergoes hibernation. Model % refers to the set truncation factor and PS indicates post-stratification measures were included.

Descriptive parameters of the nocturnal lemur populations of Sainte Luce. Global (S7, S8 + S9).

Species	Year	*Total Effort (m)*	*n*	*N*	*N LCI*	*N UCI*	N_s	$E_{(s)}$	*D / Ha*	D_s / *Ha*	*EnR / km*	P_a	*GOF-KS P*	*Model*
Avahi meridionalis	2011-2012	104,310	362	1281	793	2069	740	1.73	2.062	1.190	3.38	0.54	0.943	Hazard Rate + Single Polynomial + 2.5% + PS
	2013-2014	61,696	90	512	325	806	303	1.64	0.824	0.502	1.41	0.55	0.752	Hazard Rate + Single Polynomial + 3% + PS
	2015-2016	66,441	108	692	442	1082	404	1.64	1.114	0.679	1.89	0.63	0.529	Hazard Rate + Single Polynomial + 1% + PS
	2017-2018	60,433	100	480	348	663	330	1.40	0.774	0.551	1.57	0.72	0.567	Hazard Rate + Single Polynomial + 5% + PS
Cheirogaleus thomasi	2011-2012	53,161	157	946	766	1168	–	–	1.524	–	2.95	0.39	0.833	Hazard Rate + Single Polynomial + PS
	2013-2014	39,942	129	876	658	1167	–	–	1.411	–	3.23	0.36	0.894	Hazard Rate + Single Polynomial + PS
	2015-2016	34,104	124	827	639	1069	–	–	1.332	–	3.46	0.58	0.881	Hazard Rate + Single Polynomial + 5% + PS
	2017-2018	36,537	156	1291	970	1717	–	–	2.079	–	3.83	0.61	0.940	Half Normal + COS + 10% + PS
Microcebus tanosi	2011-2012	104,310	67	243	183	324	–	–	0.394	–	0.59	0.40	0.685	Hazrad Rate + Single Polynomial + 7.5%
	2013-2014	61,696	46	208	157	275	–	–	0.340	–	0.71	0.76	0.685	Hazard Rate + Single Polynomial + 5%
	2015-2016	66,441	37	260	165	409	–	–	0.420	–	0.64	0.53	0.997	Hazard Rate + Single Polynomial + 2.5% + PS
	2017-2018	60,433	34	163	99	269	–	–	0.264	–	0.56	0.53	0.813	Half Normal + COS + PS

Notation

n = Number of observations detected
N = Population estimate
N UCI and N LCI = Upper and lower confidence limit for the estimated population
N_s = Number of groups
E_s = Mean group size
D/Ha = Density of animals per hectare
D_s/Ha = Density of groups per hectare
EnR/km = Encounter rate per kilometre
P_a = Probability of detecting an animal or group within the survey area
GOF-KS p = Goodness of fit, Kolmogorov-Smirnov test significance value
Model = Model definition providing the best fit. Includes key function series expansion, truncation values and post stratification

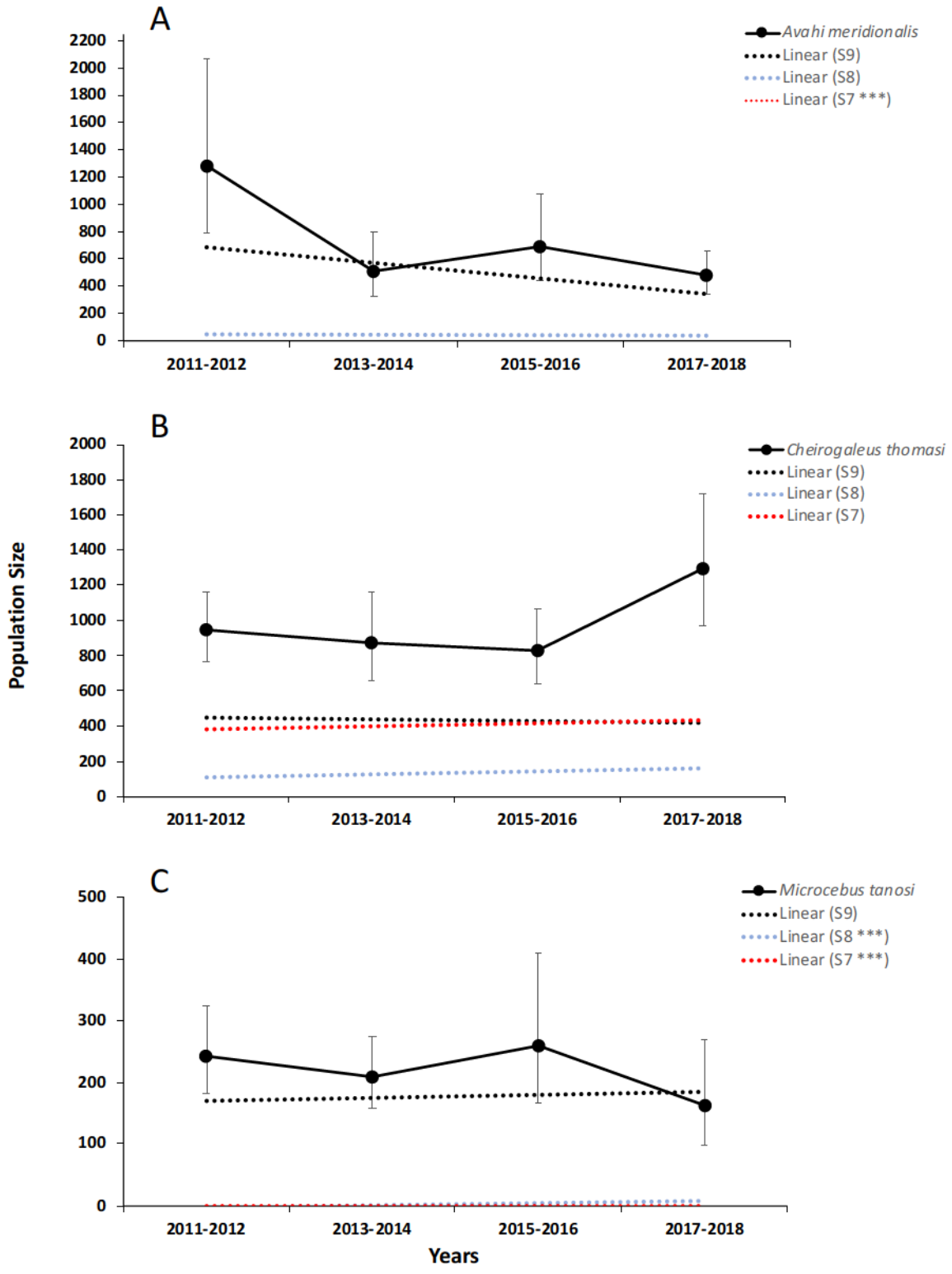

Figure 30 – Population trends of the three nocturnal lemur species in the littoral forest fragments of Sainte Luce based on distance sampling results. Data is combined into two-year sets to improve population estimates. **A**) *Avahi meridionalis*, **B**) *Cheirogaleus thomasi* and **C**) *Microcebus tanosi*. Black dots with a thick bold line indicate the global trend (S7, S8 and S9 data combined). ***Represent cases where observations were too limited to produce reliable population estimates.

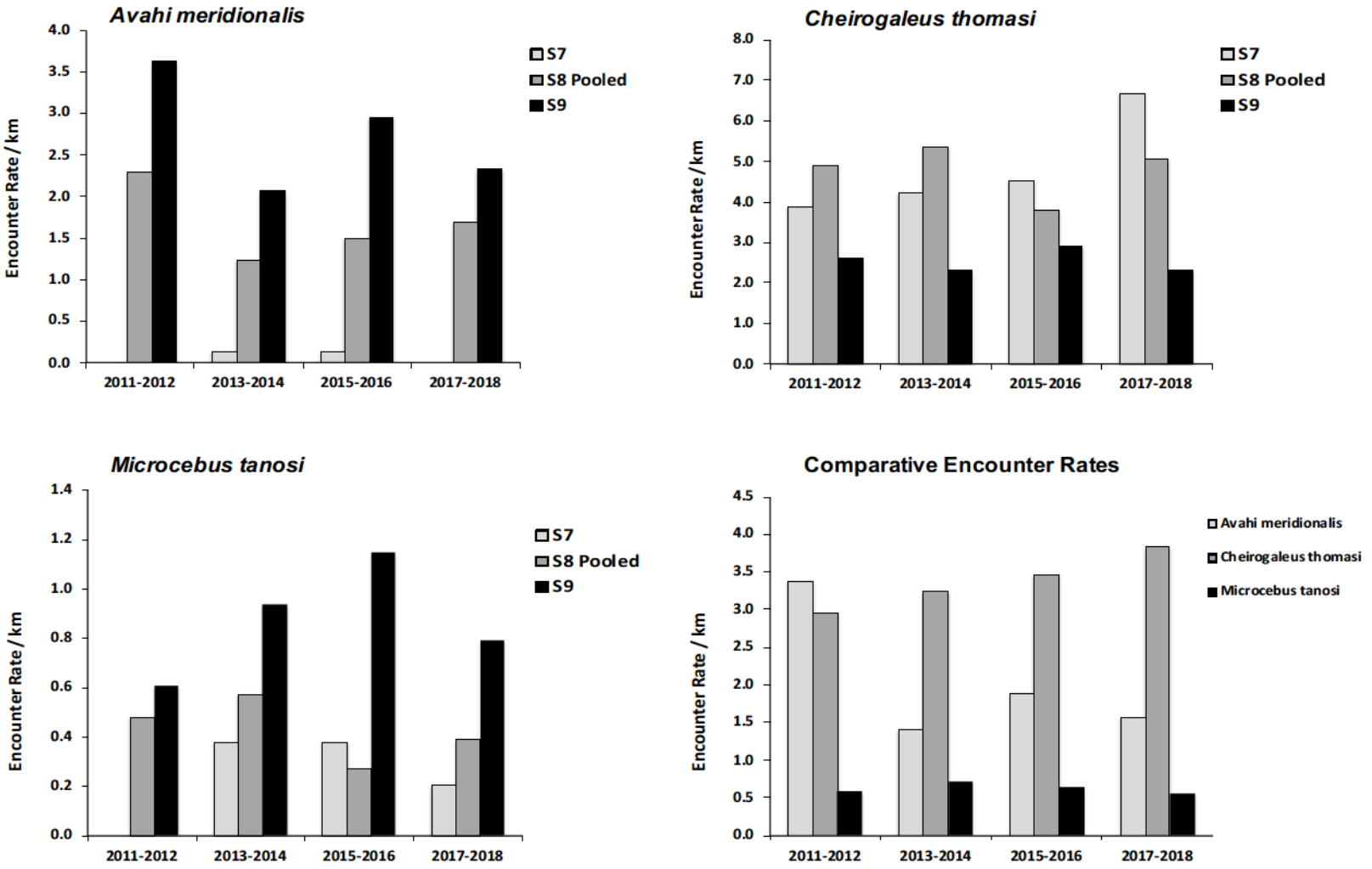

Figure 31 – Encounter rates for each of the three nocturnal lemur species in littoral forests fragments S7, S8 and S9. **A**) *Avahi meridionalis*. **B)** *Cheirogaleus thomasi* (adjusted for seasonality). **C)** *Microcebus tanosi*. **D)** A global comparison of species' encounter rates, representing general population trends. Encounter rates based on the limited transect repeats for S17 are: *A. meridionalis* 5.6 groups/km (n=4), *C. thomasi* 5.2 ind/km (n=1) and *M. tanosi* 0.8 ind/km (n=4).

Statistical Analysis

Analysis of annual observation data found no significant difference between the overall number of *A. meridionalis* recorded across the study period (**Table 26**). However, observations differed significantly between fragments, with significant pairwise findings between S7-S8, S7-S9 and S8-S9 (**Table 27**). No significance was found in the interaction between the fixed effects 'Year' and 'Fragment' for fragments S7 and S8, however a trend towards significance was observed for fragment S9 (**Table 26**). Pairwise analysis revealed a significant reduction in observations between 2011-2012 and 2013-2014 (**Table 27**). In the case of *C. thomasi*, no significant trends were detected between years. In contrast, the total number of observations between fragments was again significantly different (**Table 26**), with pairwise analysis showing significance between all fragment combinations except between S7-S8N and between S8S-S9 (**Table 27**). Analysis of the interaction between 'Year' and 'Fragment' produced no significant results (**Table 26**). No overall significance was detected in the total number of *M. tanosi* observations over the study or in the number of observations between forest fragments, although a trend towards significance was observed in the latter (**Table 26**). The near significance of overall fragment variation was shown to be as a result of significant difference between S7 and S9 (**Table 27**). No overall difference was detected in the underlying relationship between 'Year' and 'Fragment'.

GLMM analysis further confirmed no significant difference in the overall number of lemur observations across the study period (F=1.778, df=3, p=0.150, n=483). However, results show that forest fragment has a significant effect on total lemur observations (F=11.999, df=2, p=0.020, n=483). Significantly more observations were recorded in S9 than in both S7 (t=4.425, df=471, p=0.008, n=483) and S8 (t=4.288, df=471, p=0.015, n=483). However, no significant difference was found between S7 and S8 (t=-0.799, df=471, p=0.425, n=483). Furthermore, analysis of the interaction between 'Year' and 'Fragment' indicates a significant change in the number of lemur observations in S9 over the study period (t=2.746, df=3, p=0.043; n=483), with pairwise results showing significant differences between 2011-2012 and 2013-2014 (t=2.433, df=471, p=0.015, n=483) and between 2013-2014 and 2015-2016 (t=-2.168, df=471, p=0.031, n=483).

Effect of Forest Protection

When the four years before and after the formal implementation of the protected areas (S8 and S9) and community resource zone (S7) in 2015 were compared, no significant difference was detected in either the total number of lemur observations (F=1.486, df=1, p=0.223, N=483), or in the number of observations of any individual species (**Table 26**). No significant interactions were

found between individual forest fragments and the pre- and post-protective measures, with regards to each of the study species and the lemur communities as a whole.

Table 26.

GLMM model output with analysis of each fixed effect and interaction (*) for the three nocturnal lemur species over the eight-year study period (2011-2018). Significant results in bold.

Species	Fixed Effect		*F*	df	P	*n*
Avahi meridionalis	Year		0.195	3	0.900	483
	Fragment		69.804	2	**<0.001**	483
	Year*Fragment	S9	2.270	3	0.080	483
		S8	1.404	3	0.241	483
		S7	0.929	3	0.427	483
	Effect of Protection		0.577	1	0.448	483
Cheirogaleus thomasi	Year		0.151	3	0.929	284
	Fragment		4.514	3	**0.004**	284
	Year*Fragment	S9	1.117	3	0.342	284
		S8 N	0.341	3	0.796	284
		S8 S	0.371	3	0.774	284
		S7	0.367	3	0.777	284
	Effect of Protection		0.261	1	0.610	284
Microcebus tanosi	Year		0.562	3	0.640	483
	Fragment		2.512	2	0.082	483
	Year*Fragment	S9	0.767	3	0.513	483
		S8	0.478	3	0.698	483
		S7	0.429	3	0.732	483
	Effect of Protection		0.130	1	0.719	483

Table 27.

Pairwise comparisons based on the GLMM model estimates showing all significant results, including results showing a trend towards significance (*). *t* values indicate direction of result.

Species	Fixed Effect	Pairwise comparison	*t*	df	P	*n*
Avahi meridionalis	Fragment	S7 - S8	-7.485	471	**<0.001**	483
		S7 - S9	-9.387	471	**<0.001**	483
		S8 - S9	-4.194	471	**0.022**	483
	Year * Fragment (S9)	2011/12 - 2013/14	2.552	471	**0.011**	483
Cheirogaleus thomasi	Fragment	S7 - S8S	3.046	268	**0.003**	284
		S7 - S9	2.509	268	**0.013**	284
		S8N - S8S	2.637	268	**0.009**	284
		S8N - S9	2.028	268	**0.044**	284
Microcebus tanosi	Fragment	S7 - S9	-2.228	471	**0.026**	483

Discussion

The results of this study affirm the dynamic nature of population level processes, revealing differentiated trends between each focal species and across each of the study forest fragments. Whilst in general all three species appear relatively stable; no single factor fully explains the variation in observed trends. Species demographics appear to fluctuate independently between fragments, irrespective of size, paralleling observations made by Ganzhorn et al. (2008) in Mandena. These differentiated species-specific trends highlight the complexity of population dynamics within fragmented habitats (Harrison and Bruna, 1999; Debinski and Holt, 2000; Henle et al, 2004; Erhart and Overdorff, 2008) and emphasise the need for carefully considered conservation management strategies (Boyle and Smith, 2010). Furthermore, this study found no evidence for the presence of either *Hapalemur meridionalis* or *Cheirogaleus major* in the study fragments, despite previously reports (Ellis, 2003; Ganzhorn et al, 2008; Malone et al, 2013). It must now be considered highly unlikely that either species persists in Sainte Luce, underscoring the real threat of lemur extirpation. This analysis concludes that local effects have a profoundly significant influence on the population dynamics of nocturnal lemurs and that generalized predictions based on forest size, especially at small scales, may be too simplistic to describe community level patterns. Whilst forest patch size in general parameterizes primate population size (Ganzhorn, 1998; Ganzhorn et al, 2000; Henle et al, 2004; Harcourt and Doherty, 2005; Wahungu et al, 2005; Boyle and Smith, 2010), it does not necessarily determine short-term population trend. Instead, species demography appears to be highly specific and influenced by differentiated anthropogenic pressures and local phenomena. However, the negative long-term effects of inbreeding depression may be inevitable in smaller isolated fragments, although effects may be too subtle to accurately detect in broadly modelled population data.

This study confirms that the larger bodied *A. meridionalis* is in imminent danger of extirpation in forest fragment S7 (Ganzhorn et al, 2008). Furthermore, the sub-population in S9 appears to have undergone a substantial decline between 2011-2014. This decline is also mirrored in the much smaller sub-population in S8, suggesting a broader mechanism might be responsible for the observed trends given their shared management status, although the driver is unclear. Mean group size also appears to have decreased over the course of the study, most notably in S9, indicating a possible reduction in birth rate. Although further investigation is required to understand this phenomenon, it has also been observed in other lemur species (Erhart and Overdorff, 2008). The limited number of observations in S7 is also not easily explained by conventional factors associated with populations dynamics such as patch size or diet (Ganzhorn et al, 1995; 2000;

Struhsaker, 1997; Chapman et al., 2002; Lehman et al., 2006) given that floral diversity in the fragment remains high (Hyde Roberts, unpub.). In fact, the relatively large size of S7 and its proximity and connectivity to another large forest block (S6) suggests that these two fragments combined could maintain a relatively large sub-population of *A. meridionalis*. Together, the twin fragments S6 and S7 (436ha) are larger in size than S9 (368ha), which supported an estimated 360 individuals at the end of 2018. *Avahi* are also known to persist in even tiny vestiges of forest (<10ha) in both Sainte Luce (S. Hyde Roberts. pers. obs) and Mandena (Ganzhorn et al, 2008).

However, forest structure in S7 is notably degraded, with the average canopy height and coverage lower than in the other study fragments (**Table 24**). This observation supports the hypotheses that population density of this species is positively correlated with the presence of larger trees (Ganzhorn et al, 2008; Norscia, 2008). As a folivore (Thalmann, 2003; Norscia et al, 2011), it seems unlikely that limited food resources could have driven the notable decline between 2011-2014, given the high plant diversity in the area (Lowry and Faber-Langdoen, 1991; Dumetz, 1999; Cadotte et al, 2002; Consiglio et al, 2006). In fact, *A. meridionalis* is a relative generalist with only moderate leaf selectivity (Norscia et al, 2011). It has also been postulated that the minimum area requirement for folivorous and omnivorous species may be smaller than for species with other dietary needs (e.g. frugivores) (Ganzhorn et al, 2000), with resources expected to be more evenly distributed and reliable, particularly in evergreen forests. Furthermore, low-level forest disturbance, a notable characteristic of littoral forests, has been demonstrated to potentially benefit some folivorous species (e.g. *Avahi* spp.) by improving the nutritional quality of foliage (Chapman et al, 2002; Ganzhorn, 1992; Ganzhorn, 1995).

Although the designation of S7 as a community resource forest could be predicted to negatively impact lemur communities (de-Almeida-Rocha et al, 2017), affecting forest structure and increasing the number of woodsmen and potential hunters present in the forest, *A. meridionalis* appear to have been scarce in this fragment for a far longer period of time (Ganzhorn et al, 2008). The most parsimonious explanation for the anomalously small sub-population of *A. meridionalis* in S7 and the declines in both S8 and S9 is therefore a combination of historical and on-going hunting pressure. Similarly, the absence of *E. collaris* from S7 is likewise attributed to hunting, and as the next largest and conspicuous species it is plausible that *A. meridionalis* has been similarly depleted. Local elders (six individuals including the ex-Chef d'Fokontany and local guides) estimated the disappearance of brown lemurs from the S6/S7 forests to be c.a. 1960 and confirmed that hunting pressure was high in these forests until as recently as 2010. For the sub-population of *A. meridionalis* in S7 to remain so low since at least 2004 (Ganzhorn et al, 2008),

it suggests that either the species is very slow to recover from severe historic exploitation or indicates that some level of hunting pressure continues in the community resource forests. The severe recent degradation of the forest as a result of intense community harvesting could also be hindering species recovery, as large trees are removed, and forest structure is impacted (Ganzhorn et al, 2007; Norscia, 2008). In light of these results, the Endangered *A. meridionalis* should be considered a priority species for conservation efforts and future monitoring in Sainte Luce.

No significant difference was detected in the total number of *C. thomasi* over the course of the study, indicating that the population as a whole in Sainte Luce is relatively stable. Despite this however, the dynamics between the forest fragments and the isolated sub-populations differ markedly. In general, estimated sub-population size does not adhere to the expected pattern whereby a larger fragment supports a larger population (Harcourt and Doherty, 2005). S7 currently supports a larger estimated population of *C. thomasi* than S9, despite being 122ha smaller in size. Similarly, S8 supports a substantial population whilst only being roughly a fifth of the size of S9. Although larger forests should provide a greater quantity and diversity of resources, the effect of fragment size on population density is complicated by a range of other inter-acting environmental, ecological and genetic factors (González-Solís et al, 2001; Ramanamanjato and Ganzhorn, 2001; Marsh, 2003; Rovero and Struhsaker, 2007; Irwin, 2008; Malone et al, 2013). Notably, the sub-population of *C. thomasi* in S7 appears to be increasing despite intense logging and natural resource removal. This observation suggests that the species may to some extent tolerate moderate to severe forest degradation. However, this interpretation contrasts with the conclusion of Ganzhorn et al. (2008), who surmised that *Cheirogaleus* spp. responded negatively to habitat degradation. Although, it seems that two distinct Cheirogaleid species (*C. major* and *C. thomasi*), now understood to exhibit specific responses, may have been considered jointly in that study.

Although there is no conclusive explanation for the unexpected positive trend for *C. thomasi* in S7, the seemingly rapid increase in population size and the timing suggests the expansion is linked to the phenomenon of habitat degradation and local forest management policy. Given its degraded nature, S7 could be expected to exhibit relatively limited fruit availability and increased patchiness in relation to more intact forest (Campera et al, 2014), however reduced competition for fruit resources from other fauni-frugivorous lemur species (e.g. *E. collaris*) may also be significant. Similarly, a shift towards a more invertebrate based diet seems unlikely given their reduced importance in the diet of *Cheirogaleus* spp. (Fietz and Ganzhorn, 1999; Hladik, 1979; Lahann, 2007). Although degradation may be increasing this dietary resource (Corbin and

Schmid, 1995; Malcolm, 1997; Passamani and Rylands, 2000; Spironello, 2001) the *M. tanosi* sub-population does not seem to be similarly exploiting it. Alternatively, a potential increase in the nutritional content of plant food resources, associated with habitat degradation and increased light levels may be a contributing factor (Ganzhorn, 1992; Ganzhorn, 1995; Chapman et al, 2002; Atsalis, 2008) as logging exposes understory trees to increased levels of sunlight, which is positively correlated with fruit production (Ganzhorn, 1995). Ultimately however, despite the apparent increase in the number of *C. thomasi* in S7, continued degradation is likely to negatively impact the species in the long-term. The loss of large trees and sufficient sleeping and hibernation sites may eventually reverse the positive population trends and the increased temperatures associated with degraded and edge habitats may begin to negatively impact hibernation patterns (Ganzhorn and Schmid, 1998; Lehman et al, 2006b). Given that such an important sub-population exists in S7, within the proposed QMM mining footprint (Temple et al, 2012), future mitigation work will be required if substantial losses are to be avoided.

The sub-population of *C. thomasi* in S9 appears to be the most stable of the three study fragments, indicating that perhaps the fragment is the most ecologically balanced and potentially near its carrying capacity (Janson and Chapman, 1999). The formal protection of the fragment appears to have had little impact on the sub-population in S9 so far. The S8 sub-population has also seemingly expanded in recent years, although fluctuates over the study period. Although the exact driver of the trend is unclear, the sharp boundary between the forest edge and savannah like matrix environment to the west of the fragment has been heavily planted with non-native trees, and particularly *Grevillea robusta*. It is now common to see large numbers of dwarf lemurs feeding on flowers and nectar in these maturing plantations. Large numbers of C. *thomasi* have also been observed feeding on *G. robusta* outside of natural forest at Lokaro (S. Hyde Roberts, pers. obs). These plantations likely provide a highly abundant and nutritious resource as the lemurs emerge from hibernation. Capitalizing on such resources could provide an additional management tool in future conservation efforts for this Endangered species along with a number of other lemurs (Ganzhorn et al, 1991; 2020; Eppley et al, 2015).

The *M. tanosi* population in Sainte Luce appears to be small but stable with no significant overall change in the number of observations across the study, or made between forest fragments. However, population modelling was inhibited by the very low number of observations made in both forest fragments S7 and S8. Both population estimates and encounter rates are much lower than for the other two nocturnal species, and indeed other *Microcebus* species in proximal littoral forests (Ganzhorn et al, 2008; Malone et al, 2013). The limited number of *M. tanosi* observations

is surprising, and it was initially hypothesised that mouse lemurs would likely be the most abundant lemur species in Sainte Luce, given their small size, social structure, broad ecological niche and small home ranges (Radespiel, 2000; Andrianasolo et al, 2006; Lahann, 2007; Génin, 2010; Karanewsky and Wright, 2015; Hending et al, 2017). Furthermore, Sainte Luce is missing several important predators (e.g. *Accipiter henstii* and *Cryptoprocta ferox* – Hyde Roberts, unpub. data) and whilst it has been postulated that the high density of mouse lemurs at Petriky may be the result of overcrowding, due to a lack of predator diversity (Malone et al, 2013), this is evidently not the situation in Sainte Luce. However, results suggest that *M. tanosi* is relatively tolerant of habitat disturbance and are regularly observed in degraded habitats and at forest edges in Sainte Luce and even around the research field station. Although population estimates are based on a limited number of survey observations, the findings of this study match earlier results published by Ganzhorn et al. (2007) and explain the very low trapping success (max. 0.54%) using standard Sherman traps (Hyde Roberts, unpub. data). In the Protected Area of Tsitongambarika, the large expanse of lowland rainforest on the west of the study site, the species also seems to occur at very low densities (G. Donati. pers. comm).

This study concludes that distance sampling, following the standard 'Buckland' method and using line transects and perpendicular distance is well suited to the study of larger nocturnal lemur species such as *Avahi* and *Cheirogaleus*, but is problematic for the study of mouse lemurs, at least in Sainte Luce. Modelling accuracy is dependent on generating sufficient sample sizes, which is particularly challenging for rare or low-density species (Thompson, 2013), as appears to be the case for *M. tanosi*. Furthermore, even under ideal conditions, the method is known to produce relatively high standard errors, making small scale population fluctuations difficult to identify, particularly when the number of observations is limited (Plumptre and Cox, 2006). The method also relies on a series of crucial assumptions, including a perfect detection of all animals at distance 0m from the transect line and that animals do not move quickly enough to later appear again ahead of the survey team (Buckland et al, 2001; 2015). Although it is conceivable that individual animals could be missed high in the canopy, the overall lack of *M. tanosi* observations suggest that double counting is not a critical problem. The longitudinal nature of the project and high survey effort also suggests that the low number of mouse lemur sightings is a valid representation of the mouse lemur population in Sainte Luce.

It is plausible that the line transects used in this study, and specifically their positioning, which bisect the forest fragments, are not wholly adequate for the accurate determination of the *M. tanosi* population in the littoral forests of Sainte Luce, finding some accord with both Müller et al. (2000)

and Radespiel et al. (2001). It is becoming increasingly clear that the demographics of mouse lemur species vary considerably (Ganzhorn et al, 1998; 2008; Weidt et al, 2004; Rakotondravony and Radespiel, 2009; Herrera et al, 2011; Schäffler and Kappeler, 2014; Steffens et al, 2016), and distance sampling may not be the most appropriate means of determining population size in habitats where the target species exist at low density. It is also possible that individuals foraging near or at the forest edge could have been missed. However, given the highly fragmented nature of the littoral forests, the interior of most fragments is barely more than a few hundred metres from either a habitat edge or a forest clearing, and edge effects likely penetrate entire fragments. Similarly, whilst all mouse lemur species are thought capable of entering short bouts of daily torpor during the winter months and reducing activity levels (Petter-Rousseaux, 1980; Ortmann et al, 1996; Schmid, 2000; Andriambeloson et al, 2020), the number of observations in this study was largely consistent throughout the year.

The designation of protected areas and community use zones in 2015 have so far shown no significant impact on the lemur communities, although it is conceivable that the benefits will take longer than four years to significantly manifest in population data. These findings echo those of a recent global assessment of biodiversity within protected areas (Beaudrot et al, 2016), which found that of 24 primate study populations across Africa and southeast Asia, none were found to be increasing. It is also important to note here however, the critical role of protected area management, enforcement and effectiveness, which is highly unequal between sites. The measures now attributed to each fragment in Sainte Luce have been long proposed (Temple et al, 2012), but only during 2015 were formal measures introduced and practically enforced on the ground. Until this point, logging and resource collection was common practice across all fragments, however S7 was already in a highly degraded state by 2006 (G. Donati. pers comm). Once measures were introduced, logging and community use in the protected fragments ended abruptly and with the installation of an access bridge, resource collection and activity in the community forest increased further (S. Hyde Roberts. pers. comm). Whilst the total number of lemur observations in the community resource zone has also increased since 2015, due to burgeoning numbers of *C. thomasi*, the future of this fragment and its lemur community remains bleak. The results of this study clearly confirm that the response of the lemur community to habitat degradation and fragmentation is complex and nuanced (Merenlender et al, 1998; Rendigs et al, 2003; Balko and Underwood, 2005; Lehman et al, 2006; Marsh et al, 2013; Eppley et al, 2020; Gould et al, 2020), varying between species, but also that forest management policies can play an important role in conserving threatened lemurs (Gorenflo et al, 2011).

An additional source of variation in the dataset may also stem from stochastic events. Over the course of this study, 15 major tropical storms and cyclones have passed within 500km of Sainte Luce, seven within 200km and five passing within 100km. The epicentre of three of these major weather events passed within 20km of the study site (Cyclones Bingiza 2011, Dando 2012 and Harunga 2013). However, cyclones Bingiza, Giovanna (2012), Haruna (2013) and Enawo (2017) are the most likely storms to have had a detrimental impact on lemur populations, given both their proximity and severity. Cyclones are known to cause severe negative impacts on lemur populations, causing direct damage to habitats, destroying important fruit crops (Ratsimbazafy et al, 2002), and potentially disrupting reproductive schedules (Wright, 1999; Wright et al, 2005; Dunham et al, 2011). Such events may have added to the noise in the population trend data and possibly contributed to observed fluctuations.

In conclusion, this study demonstrates the importance of long-term population monitoring for lemurs and other nocturnal primates and highlights the critical importance of local phenomena and forest management strategy for species conservation. Insights gained from long-term studies can provide early diagnosis of declines in vulnerable populations and help to pinpoint causal mechanisms. In the case of Sainte Luce, these results are particularly salient, as community demand for natural resources grows, putting additional pressure on remaining forests. Furthermore, proposed mining operations are expected to clear an estimated 58% of existing forest cover (value obtained using GIS tools and based on Temple et al, 2012), further isolating lemur sub-populations. However, this study indicates that even modestly sized forest fragments (<100ha) can provide vital refuges for threatened nocturnal lemur species and should not be overlooked in environmental planning. Each of the three nocturnal species in this study lacks the dispersal capability to traverse between isolated fragments and strategies must therefore attempt to maximise habitat connectivity to encourage dispersal between larger forest fragments. A range of conservation tools including habitat corridors, habitat restoration and translocations are likely to be necessary in the short to medium term future in order to maintain the genetic viability of the lemur community in Sainte Luce long-term.

CHAPTER 7

An appraisal of biodiversity in the littoral habitats of Sainte Luce

Introduction

Madagascar supports a globally important biodiversity characterized by extensive species richness, high levels of endemicity and broad phylogenetic clustering within a select range of taxonomic groups. The families of plants and animals represented on the island reflect the islands ancient origin and long isolation from other landmasses (Fooden, 1972; Krause et al, 1997; Vences, 2004; Yoder and Nowak, 2006; Upchurch, 2008; Reeves, 2014). Numerous new species are still regularly described across a range of taxa (lemurs; bats; rodents; amphibians; reptiles; palms) (e.g. Goodman et al, 2012; Hotaling et al, 2017; Ratsoavina et al, 2017; Eiserhardt et al, 2018; Jansa et al, 2019; Scherz et al, 2019) whilst other groups remain relatively unstudied (e.g. freshwater fish, arachnids, moths). Such high species level diversity has revealed Madagascar to be an engine of evolution, with its biodiversity distributed across its varied landscapes and habitat types. However, the island has experienced dramatic environmental change over the past century (Harper et al, 2007; Gorenflo et al, 2011; Vieilledent et al, 2018) and the burgeoning threats posed to its native flora and fauna make Madagascar an important global conservation priority (Myers, 2000; Mittermeier et al, 2005).

Against this backdrop of widespread habitat loss (Green and Sussman, 1990; Nelson and Horning, 1993), the littoral forests have long stood out as a national priority (Ganzhorn et al, 2001; Ingram and Dawson, 2005; Bollen and Donati, 2006; Consiglio et al, 2006). Once believed to occupy much of the coastal fringe of eastern Madagascar, the littoral forests now persist only in small isolated fragments (Green and Sussman, 1990; de Gouvenain and Silander 2003). Despite their greatly reduced extent, estimated at around 10% of their original distribution (Myers et al, 2000; Consiglio et al, 2006), the eastern littoral forests are known to harbour about 13% of Madagascar's total native flora, with an estimated 25% of these endemic to littoral habitats (Du Puy and Moat, 1996; Schatz et al, 2000; Moat and Smith, 2007). Littoral ecosystems also support distinct animal communities with endemic invertebrates and assemblages of vertebrates (Ganzhorn et al, 2000; Watson et al, 2005; Schütte and Razafindraibe, 2007; Ganzhorn et al, 2008). However, relatively few littoral forests exist within the protected areas network (Consiglio et al, 2006; Goodman et

al, 2019). Therefore, given the status of the littoral forests as a whole in Madagascar, their importance for supporting biodiversity and their vastly diminished distribution, this habitat type urgently requires the full attention of the conservation community.

In the extreme southeast, the littoral forests of Sainte Luce are considered to be the most intact (Rabehevitra et al, 1996; Dumetz, 1999; Temple et al, 2012), and support the greatest biodiversity. Although Sainte Luce shares many similarities with nearby forest patches at Mandena, and to a lesser extent Petriky, the plant and animal communities they support differ critically in both composition and abundance (Watson et al, 2005; Jenkins et al, 2007; Ramanamanjato, 2007; Ganzhorn et al, 2008). The Sainte Luce formations currently comprise of 17 disconnected forest fragments, ranging in size from between 6ha to 350ha and cover a total estimated 1500 hectares (**Fig. 32**) (Ramanamanjato, 2007; Vincelette et al, 2007b and see **Chapter 2**, **Study area**). The human community of Sainte Luce is comprised of three hamlets – Ambandrika, Ampanasatomboky and Manafiafy – with a combined total population of approx. 2500 (Berina. *Chef de Fokontany*. pers. comm), who all rely to some extent on natural forest resources. Furthermore, the forests also support the communities of Ebakika to the north and Mahatalaky and Tsiharoa Ampasy to the west. As a result, significant pressure is exerted on remaining forest resources for food, construction materials and livelihoods (Vincelette, 2003; Bollen and Donati, 2006; Rasolofoharivelo, 2007; Hogg et al, 2013). Today, the remaining fragments are differentiated in terms of size and condition, in part due to their individual extraction histories. The area is also subject to a well-documented, but controversial mining operation initiated by QIT Madagascar Minerals (QMM), a subsidiary of the large international corporation Rio Tinto, who plan to exploit the areas mineral rich substrate to extract titanium-iron oxide, or ilmenite (Vincelette, 2003; Ganzhorn et al, 2008; Watson et al, 2010; Temple et al, 2012). As a result of the mine's presence, the area has received a relatively extensive environmental impact assessment and the flora and fauna has been well characterised (Lowry and Faber-Langendoen, 1991; Lewis Environmental Consultants, 1992b; Rabevohitra et al, 1996; Du Puy and Moat, 1998; Dumetz, 1999; Ganzhorn et al, 2007).

In this chapter I provide an update of the earlier review of Bollen and Donati (2006) who assessed the conservation status of the littoral forests, with an emphasis on Sainte Luce. The initial review prognosticated, along with others (Ganzhorn et al, 2001; Harper et al, 2007), that the southern littoral forests are likely to lose numerous endemic plant and animal species in the near future. Since a substantial amount of time has now elapsed and local circumstances have changed in many ways, now is an appropriate time to review the situation in Sainte Luce. Furthermore, the

past three decades have seen an astonishing development in our ability to understand the underlying relationships between species and our ability to identify novel taxa based on genetic evidence. It is now possible to contrast the biodiversity measured during the earliest environmental studies (Lewis Environmental Consultants, 1992b) with our modern understanding. This update is based on varied research projects and personal observations amassed between September 2014 until present, and incorporates the findings of published works, interactions with other field researchers and communications with local stakeholders. Whilst the previous review focused its attention on the contemporary drivers of forest loss and role of seed dispersers, this update concentrates on the broader threats and impacts on local biodiversity. Furthermore, it is possible to reflect on the progress that has been made based on the conservation recommendations set out by Bollen and Donati (2006), and I detail an updated set of conservations priorities for the coming decades.

Major threats

In general, the threats facing the natural flora and fauna of Sainte Luce are largely unchanged from those outlined by Bollen and Donati (2006), i.e. a reliance on slash and burn agriculture (or *tavy*), unsustainable levels of selective resource harvesting and hunting. The imposing threat of mining activity also remains. Since the initial review the human population of Sainte Luce has increased substantially, from 1,238 (Foara. *Chef de' Fokontany*. pers. comm) in 2006 to 2,667 at the latest census in 2019 (Berina. *Chef de' Fokontany*. pers. comm). Coincident with this rapid population growth is an increased demand for natural resources. An estimated 90% of the energy needs of rural communities around Tolagnaro are met from firewood (QMM, 2001). In past decades, many local people reliant on the littoral forests have collected dead wood rather than cutting live trees for energy usage (QMM, 2001). This practice is thought to extol a lesser impact on forest structure and biodiversity than standard logging, yet the felling and use of live trees, often disguised as dead wood collection was common practice by 2000 (G. Donati. pers. comm). However, the legal protection and status change of several forest fragments as of 2015 (see **Chapter 2**, **Study area**) has resulted in a rapid shift in local practices. Bollen and Donati considered shifting agricultural practices to be the greatest and most immediate threat to littoral forest, however unsustainable logging and clear felling are currently having a devastating impact and now pose a very serious risk to the littoral forests and biodiversity of Sainte Luce.

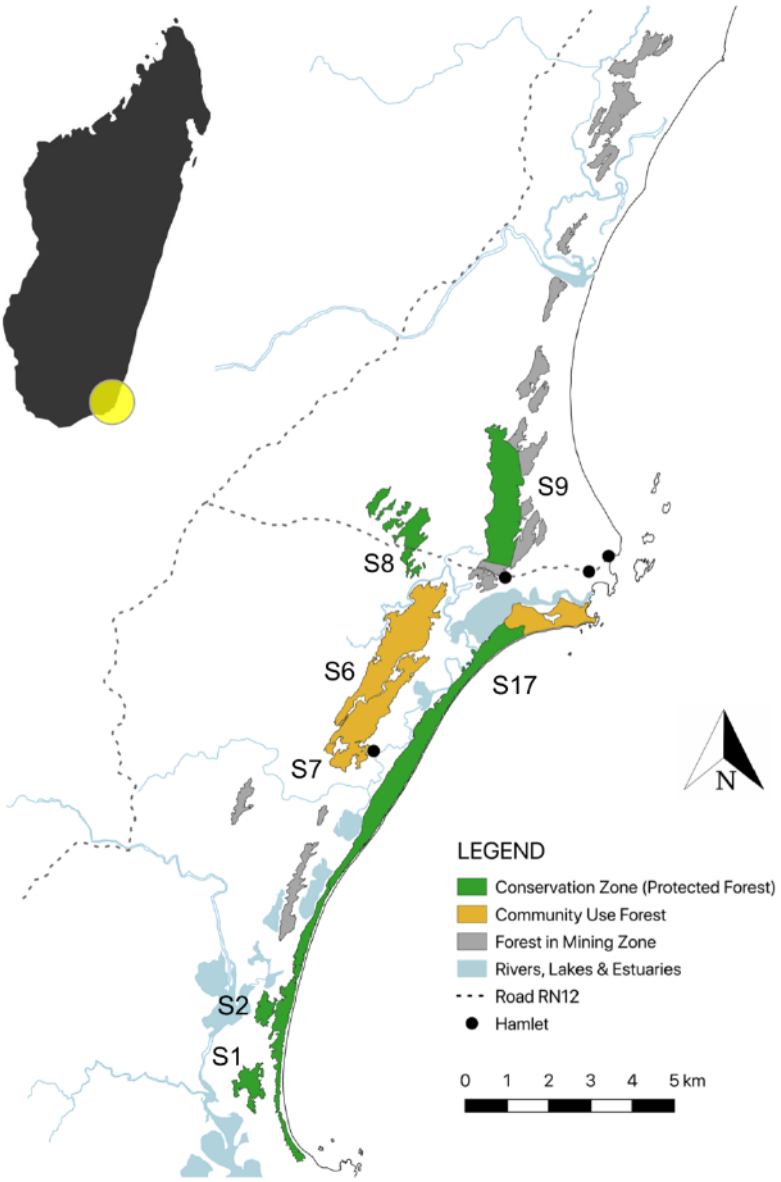

Figure 32 – The relative position of the Sainte Luce forest fragments, with both the Conservation Zones (CZ's) and Community Resource Zones (CRZ's) highlighted. *Fragments S1 + S2 are earmarked for restoration.

It is evident from satellite imagery that forest cover declined notably between 2000 and 2010 (see **Chapter 2**, **Study area**), with approximately 220ha lost. However, declines appear to have stabilized between 2010 to 2020 and ground observations reveal that although the forest boundaries are largely intact, the forests beyond the CZ's are being severely degraded internally. Whilst difficult to detect from satellite imagery, it is clear that the threat to the forests has shifted from large scale clearance, to a rapid reduction in forest quality. Logging activity is chronic and unregulated inside the community resource zones (CRZ) S6, S7 and in areas of S8 and S9 beyond

the proposed conservation zones (CZ) (**Fig. 32**). This is partly a consequence of a greater need for firewood and construction materials associated with the growing human populations. However, increased logging activity appears to be catalysed by a number of key factors besides the increased population; the lack of an effective resource management system within the CRZ, an acknowledgement by the community that part of the forest may be destroyed by mining activity in the future regardless of their actions now, and a lack of a sense of ownership of the forests emanating from how forest policies were initially decided (Holloway, 2013). Since the formal establishment of the CRZ's in 2015, a new community has appeared on the southeastern border of fragment S6, the floodplain between S6 and S17. This new hamlet comprises of around 30 houses and it largely dependent on resources from the CRZ. At present, there are no known commercial operators exploiting resources in Sainte Luce for export to Fort Dauphin, although some woodyards occasionally order timber through wealthy mediators (E.M. Ellis. pers. comm). However, commercial extraction was considered a major issue in 2000-2001, coinciding with dramatic forest clearance, highlighting its potentially devastating impact. In contrast, logging has noticeably reduced inside the proposed CZ's (S. Hyde Roberts. pers. obs), indicating that the protected forests or 'avoidance zones' as they are described in official mine literature, are being largely respected and the scheme of QMM is working. This observation matches with claims made elsewhere in Madagascar, indicating that official protection can substantially slow forest loss (Gorenflo et al, 2011).

In the short-term, utilitarian species are most at risk as demand for specific resources increases with population size. In Sainte Luce, many of these are directly related to fisheries, with roughly 80% of households engaged in related activities to some degree, providing the primary livelihood for 67% of households (Holloway, 2013). As a result, materials such as vines and palms used in the manufacture of lobster traps have become very rare, and local populations of *Flagellaria indica*, *Dypsis saintelucei*, *Dypsis prestoniana* and *Dypsis scottiana* are virtually exhausted (Bollen and Donati, 2006; Rabenantoandro et al, 2007b; Hogg et al, 2013). Sub-optimal species are now commonly used instead (e.g. *Bambusa multiplex*, *Beccariophoenix madagascariensis* and *Ravenala madagascariensis*), however durability is compromised and so resources are required more regularly. A recent assessment of the Endangered and eponymous palm *D. saintelucei* revealed a 64% reduction in the existing population over the past eight years, with only 65 known adults now remaining (Hyde Roberts et al, 2020), with most located outside of the protected forests. Similarly, there are no longer any sufficiently large and suitable trees (*Calophyllum pervillei*) for pirogue construction in Sainte Luce and new sea faring vessels must be constructed in the Anosyenne mountains to the west. The unsustainable use of natural resources

within the local fisheries industry is likely to have major implications for the local economy in coming years.

Whilst the Sainte Luce community is largely fisheries based, its reliance on agriculture is increasing (Holloway, 2013) and cassava, a hardy, drought-tolerant crop and staple of the local diet is cultivated widely. Roughly 85% of households engage in some form of agricultural practice, although it is the primary means of livelihood for only 4%, indicating that farming is largely subsistence. Despite large areas of available open ground, the borders around some fragments (most notably S6 and S8 along with its satellite remnants) are being transformed into small-scale agricultural plots, used almost exclusively for cassava cultivation. In some areas these micro-plots are encroaching into standing forest, despite being prohibited. In nutrient-depleted areas such as Sainte Luce, forested land often holds the most fertile soil and in order to exploit this, farmers often clear forest to maximise crop yield. The preferred method of land clearance is particularly destructive, with slash-and-burn cultivation known as '*tavy'* the primary approach (Kull, 2002; Kistler and Spack, 2003; Styger et al, 2007). However, rewards are short-lived as unsustainable fallow periods and repeated burning impedes soil recovery and contributes to rapid soil erosion, and desertification (Jarosz, 1993; Comte et al, 2012). The effects of rapid forest clearance on forest dynamics are long lasting. The loss of 15ha of standing forest in S8 during 1999 has not since recovered and the area is now regularly used for agriculture and zebu grazing.

Control of 'tavy' fires is problematic, particularly in windy months (September and October), and can cause widespread environmental destruction. In 2019, such a fire devastated an area of approx. 375 hectares of grass and swamp land to the east of the largest protected forest, S9. Although this event caused no harm to the littoral forest, in 2015 another large *tavy* fire to the south of S7 (Babaly. *Local Guide*. pers. comm.) resulted in the loss of 6ha of standing forest. Such fires can cause rapid and extensive habitat loss, and directly lead to the loss of Endangered and locally iconic species such as *D. saintelucei* (Hyde Roberts et al, 2020) and devastate wildlife communities. Particularly vulnerable are palms, terrestrial species with limited escape capability, ground nesting birds, invertebrate communities and species inhabiting swamps. Whilst the majority of these species are widespread and abundant across Madagascar and not deemed as being at risk species, the environmental damage caused by agricultural expansion and fire serves to exacerbate the effects of forest fragmentation and can reduce important habitat connectivity.

In Sainte Luce several animal assemblages are considered highly nested, with smaller fragments supporting a non-random subset of the communities found in larger and more intact fragments

(Ganzhorn et al, 2000; Lehtinen and Ramanamanjato, 2006). Whilst species diversity is evidently reduced in the smaller fragments, some species appear more prone to extirpation than others (Hope, 1973; Karr, 1982; Lynam, 1997; Ganzhorn et al, 2000; 2008; Lehtinen and Ramanamanjato, 2006; Watson et al, 2004; 2005; 2009), although some populations can persist for many years in small remnants before disappearing (Diamond et al, 1987; Kattan et al, 1994; Turner et al, 1996). Various traits have been proposed to explain extinction proneness (e.g. Terborgh, 1974; Diamond, 1984; Laurance, 1991; Angermeier, 1995; Davies et al, 2000; Purvis et al, 2000; Koh et al, 2004; Eppley et al, 2020), but in general those most at risk are larger, occur at low density or are rare within a community, habitat or dietary specialists and species who are intolerant of edge environments (Turner, 1996). Today the continued fragmentation and degradation of littoral forest is impacting species-area relationships and extending habitat-edge associated processes. The reduction in size and quality of contiguous forest and patch size is known to elicit negative population responses in lemurs (Ganzhorn et al, 2000; Johnson et al, 2003; Lehman et al, 2006; Donati et al, 2011; Campera et al, 2014; Bertoncini et al, 2017), forest dependent birds (Langrand and Wilmé, 1997), insectivorous mammals (Goodman and Rakotondravony, 2000), and amphibians (Vallan, 2000) whilst simultaneously impacting predator-prey and ecological dynamics (Smith and Weis, 1997). Today, the distribution of non-flying species in Sainte Luce can be considered largely determined by forest patch size, however, the pattern is affected by a number of other important threat factors.

Hunting

Bushmeat consumption in Sainte Luce was always considered relatively low-level in relation to other inland forest sites since it is primarily a fishing community reliant up on ocean resources (Bollen and Donati, 2006). However, hunting pressure has been high in the past and the legacy of past practices is still visible, reflected in the distribution of targeted animals across the Sainte Luce formations. For example, *Eulemur collaris*, the largest lemur in the area and a key ecological species, is now only present in fragments S1, S2, S8, S9, S12 and S17, and its extirpation from other fragments is likely the result of historical hunting pressure (Hyde Roberts et al, 2020). Furthermore, the recolonization of fragment S8 appears only to have occurred within the past few years, post protection. A few groups even appear to have become re-habituated to humans to a degree, with at least one group regularly spending time in close proximity to the village of Ambandrika, and another group regularly seen on the fishing beach at Manafiafy. Such behaviours are likely an indicator of relaxed hunting pressure. Similarly, the unusually small sub-population of woolly lemur (*Avahi meridionalis*) in S7 appears to be best explained by hunting (see **Chapter 6**). Whilst the hunting practices outlined in Bollen and Donati (2006) and

Randriamanalina et al (2000) appear largely to be a thing of the past in Sainte Luce, with the hunting of lemurs for bushmeat strictly prohibited under local law (*dina*), the situation can change quickly and requires monitoring.

Rare instances of hunting do still occur however, even within the CZ's and over the past couple of years several incidents have been reported. Snares have been observed set in the protected fragment S9 and on two occasions individuals *Eulemur collaris* have been seen with rope snares attached to their limbs (**Fig. 33**, **H**). Such traps are set across narrow forest paths and are reported to specifically target bird species (*Trenon australis*, *Coua gigas* and *Lophobotis cristata*), but occasionally inadvertedly snare lemurs. These traps are destroyed by local guides and members of the Polisn'ala (local forest police) when encountered. The extent of hunting for nocturnal lemurs is unknown but is not considered commonplace. In 2016 a tree was found in S7 showing the hallmarks of a nocturnal lemur hunt. The tree had been felled and worked around an obvious tree hole, a technique used to extract sheltering lemurs. In 2017 a sharpened thin stick fashioned into a skewer was found in S9, left in place inside a deep tree hole where it had been used to check for sleeping lemurs. Further anecdotal evidence was obtained during environmental education sessions at the Ambandrika school, where a surprisingly high percentage of children claimed to have eaten nocturnal lemur.

Other evidence compiled over the past few years include a series of shaped stones, used as slingshot ammunition, likely targeting frugivorous birds (e.g. *Alectroenas madagascariensis*, *Coracopsis nigra, Treron australis*); a villager and his trained dog were observed hunting tenrec species in S9 and reports of two shooting incidents at the site of the flying fox (*Pteropus rufus*) colony in S6. Evidence of a tenrec (*Setifer setosus*) kill is occasionally still observed by researchers, where the spines are removed in the forest and left behind by the hunter. Whilst it is likely that clandestine bushmeat consumption still occurs at a low level, at least in the CZ's hunting does not appear to be a major threat to any particular species at the present time. However, the situation in the more remote and less well monitored forest fragments is unclear. In Manafiafy, marine turtles (*Caretta caretta*, *Chelonia mydas*, *Dermochelys coriacea* and *Eretmochelys imbricata*) are regularly captured by fishermen and eaten throughout the year, and the one species known to nest on the Manafiafy coast (*C. caretta*) is traditionally consumed during its nesting season. The species has experienced heavy mortality rates in previous decades and the nesting population is likely on the verge of extirpation. Just a single nest was discovered along a 6.5km stretch of nesting beach between November and January in 2018.

Whilst hunting is currently a minor threat to most species, a small number (primarily snakes, birds of prey and crocodiles) still experience high levels of persecution (e.g. *Acrantophis madagascariensis, Asio madagascariensis, Crocodylus niloticus*, *Leioheterodon madagascariensis*, and *Sanzinia madagascariensis*). Since these predatory species occur at low density, persecution is likely to pose a notable threat to overall populations. The crocodile population in Sainte Luce is thought to be small, yet there have been several reported incidents of minor attacks on humans over the past five years, although no fatalities are known. In response, several local hunters are considered to be crocodile specialists and often trap crocodiles using large baited hooks. Other persecuted species are often killed opportunistically, in part out of fear, and in response to a perceived threat to livestock and children. Snakes are frequently killed. The remains of a Madagascan owl (*Asio madagascarensis*) were also recently observed on a forest trail within the protected forest fragment S8 and were apparently deliberately displayed. Finally, the threat posed from the collection of wild animals kept as pets is also negligible in Sainte Luce in recent times. Since 2014 there has been only a single instance of a lemur (*Cheirogaleus thomasi*) being kept inside a home in Ambandrika, and it was rapidly released after pressure from community members and local members of COBA (a local resource management body). After more than a decade based in Sainte Luce, with very close community ties, the SEED Madagascar research team has not heard or seen any evidence for the existence of the illegal collection of animals, either for the international animal trade or national level trafficking. However, large collections of rare herpetological species, including the Critically Endangered gecko *Phelsuma antanosy*, are known to have been illegally collected and smuggled from nearby littoral forests (H. Schneider, pers. comm).

Mining

The impact of the proposed ilmenite mine in the region provides a further overarching threat to many endangered species (Ganzhorn et al, 2001; Consiglio et al, 2006; Bollen and Donati, 2006; Watson et al, 2010; Goodman et al, 2019). Although many questions still remain unanswered with regards to the operation in Sainte Luce, works are anticipated to begin within the next decade (L. Gaylord. Pers. comm). Based on satellite imagery (CNES / Airbus 2020) and the projected mining area proposed by QMM (Temple et al. 2012) there will be an estimated 822ha loss of existing littoral forest in Sainte Luce, including the total clearance of 12 of the 17 fragments. Although the proportion and abundance of utilitarian species across each fragment is unknown, it may be assumed that a large quantity of resources valuable to the community, for either construction of medicinal purposes will be lost during the mining operation and alternatives will be required to

uphold cultural practices. Sustainably replacing resources lost during the operation will be critical, particularly as only protected areas will remain when the concession is concluded.

Alongside the installation of conservation zones (**Fig. 32**), QMM have committed to restore 225ha of littoral forest post mining (Temple et al, 2012). The location of the proposed forest is unclear but is expected to be positioned strategically to maximise regeneration and connectivity (Temple et al, 2010). In addition, large biodiversity offsets have been established away from mining zones, with the specific objective of preserving forest habitat and decreasing pressure on threatened species, many of which are shared with the littoral forests. Whilst the protection of these forests is welcome from a conservation perspective, the offsets have proved controversial in proximal communities, who feel that they are being poorly compensated for losing access to resources and ancestral lands (Seagle, 2012). Similar negative community impacts have been associated with the mine in both Fort Dauphin and Mandena (Seagle et al, 2012; Račevska, 2020). Whilst one of the mines benefits is undoubtedly the much-needed development and economic improvement, the associated investment is road infrastructure could further threaten the littoral forests and its wildlife. Roads are widely recognised as drivers of global deforestation (Goosem, 2002; Blake et al, 2008; Hoskin and Goosem, 2010; Fahrig and Rytwinski, 2009; Poor et al, 2019) and facilitated the extensive logging seen in Madagascar during the 1990s (Gorenflow et al, 2011). The development of the RN12A will increase access to the littoral forests of Sainte Luce and could trigger commercial extractive enterprises and even increase the risk from illegal wildlife traffickers. Furthermore, mining has been linked with increased radionuclide exposure and accused of encroaching into restricted environmental buffer zones (Swanson, 2019). Despite the considerable contribution to research in the local area (e.g. Lowry and Faben-Langdoen, 1991; Lewis Environmental Consultants, 1992, 1992b; Ganzhorn et al, 2007; Kling et al, 2020) the conclusions drawn on the effectiveness of current environmental measures are mixed. Whilst some practical initiatives can be considered a success (Donati et al, 2007; Campera et al, 2014; Andriamandimbiarison et al, 2015), other studies conclude that current efforts are insufficient to preserve the areas biodiversity and functional ecology long-term (Ramanamanjato and Ganzhorn, 2001; Watson et al, 2005; Bollen and Donati, 2006).

It is also now evident that important populations of species deemed conservation priorities exist within the mining footprint. A group of ten Endangered collared brown lemurs (*Eulemur collaris*) inhabit forest fragment S12 and all three nocturnal lemur species (*Avahi meridionalis*, *Cheirogaleus thomasi* and *Microcebus tanosi*) occur in the five surveyed fragments within the mining zone (S6, S7, S10, S11 and S12) (S. Hyde Roberts. pers. obs). A large population (approx.

490 individuals) of the Endangered dwarf lemur *C. thomasi* is known to inhabit forest fragment S7 (**Chapter 6**) and similar numbers likely occur in S6. The only flying fox (*Pteropus rufus*) colony in Sainte Luce is also situated in S6, and whilst the species is widespread elsewhere, this roost is one of only a handful in the Tolagnaro area known to still reside in natural forest (Jenkins et al, 2007; Hyde Roberts et al, 2016). Furthermore, fragment S7 appears to support a significant population of *Phelsuma antanosy* and 14 of the 18 known observations of the Data Deficient ghost gecko *Matoatoa spannringi* also originate from the S6/S7 forest block (SHR unpub. Data). Almost 80% of the 65 known remaining adult *Dypsis saintelucei* palms exist inside the mining zone, whilst just 15 remain inside the protected areas (Hyde Roberts et al, 2020). Bird diversity inside the main protected forest fragment S9 also appears to be lower than that within the CRZ's, (S. Hyde Roberts, unpub. data), possibly the result of years of dead wood collection impacting invertebrate communities. It is therefore becoming clear that the littoral forests within the mining zone support important biodiversity, and the larger twin fragments S6 and S7, currently CRZ zones appear particularly important.

Besides the loss of large swathes of littoral forest, the mining operation is expected to drastically alter the wider Sainte Luce landscape and greatly impact all connective and aquatic habitats within the mining footprint (Máiz-Tomé et al, 2018). Away from the forests, mining operations have also been identified as the major conservation threat to the Odonata community as a result of the increased turbidity, water pollution, siltation and eutrophication of important water bodies expected as the dredge progresses (Máiz-Tomé et al, 2018). The littoral area is considered an important hotspot for Odonata biodiversity and supports noteworthy species richness as well a high number of threatened and Data Deficient species (Máiz-Tomé et al, 2018; Hyde Roberts et al, 2019). Wetland areas are also important to a number of bird species e.g. *Gallinago macrodactyla*, *Nycticorax nycticorax* and *Porphyrio madagascariensis*, although the wider landscape is likely to be able to accommodate these. The impact on locally important economic resources such as the grey sedge *Lepironia articulata* are also unclear, as are the effects on proximal coastal environments, mangroves, lagoons and fisheries, which may be sensitive to unmitigated operational effects (e.g. disruption of important marine, brackish and freshwater breeding and feeding grounds). However, the lessons learnt from the environmental modifications made to the aquatic landscape at Mandena, during phase one of the mining project, including the damming of the Anony river (Réville et al, 2007; Swanson 2019) and the effects on the aquatic ecosystem, can potentially be transferable to Sainte Luce.

Invasive and exotic species

Habitat degradation and a fragmented landscape structure are associated with an increased threat from invasive and exotic species (With, 2002; King et al, 2011; Joshi et al, 2015; Harper and Bunbury, 2015) and the spread of non-indigenous species into insular communities and areas with high rates of endemism are a global conservation concern (Mack et al, 2000; Kolar and Lodge, 2001; Towns et al, 2006; Donlan and Wilcox, 2008). Whilst the floral community of Sainte Luce contains many cosmopolitan forest species (e.g. *Cocos nucifera*, *Ficus reflexa*, *Flagellaria indica*, *Hibiscus tiliaceus*, *Instia bijuga*, *Scutia myrtina*) due to its coastal nature, most exotic tree species (notably *Acacia mangium*, *Eucalyptus sp.* and *Grevillea robusta*) are deliberately introduced for plantation and reforestation purposes and are thought to pose little risk as invasive species. However, the introduced *Melaleuca quinquenervia* can become invasive in swampy areas (Eppley et al, 2015). In contrast, the faunal community contains relatively few alien species. Of these, the black rat *Rattus rattus* is perhaps the most problematic (Jones et al, 2008; Ruffino et al, 2009; Shiels et al, 2014) and whilst widespread throughout Madagascar (Goodman, 1995), appears to thrive in highly fragmented landscapes (Ganzhorn, 2003). Whilst there has been little evidence to indicate that *R. rattus* competes directly with native rodent, tenrec or lemur species (e.g. *Microcebus* spp.) (Ramanamanjato and Ganzhorn, 2000; Ganzhorn, 2003), diets overlap extensively (Goodman, 1995). It has been proposed that *R. rattus* may feed directly on the nestling young of mammals (Goodman, 1995), but as omnivores, are known to consume a diverse range of plants and animals and likely pose a significant threat to a wide range of species (Varnham, 2010; Harper and Bunbury, 2015; Thibault et al, 2017). On a larger scale, invasive rats can also disrupt ecosystem functioning, effecting pollination and interrupting trophic pathways, and can even lead to environmental collapse (Towns et al, 2006; Meyer and Butaud, 2007; Athens, 2009; Kaiser-Bunbury et al, 2009; Hilton and Cuthbert, 2010). *Rattus rattus* is currently found throughout all forests in Sainte Luce and more research is required to understand the impact of this species on the ecosystem.

Figure 33 – A series of photographs depicting some of the threats facing the littoral forests of Sainte Luce. **A**) An aerial view of forest fragmentation and agriculture plots to the northwest of fragment S8. **B**) An area of burnt ground between two forest remnants in the north of fragment S8. **C**) Cassava cultivation on the forest edge of S7, with an exposed *Beccariophoenix madagascariensis* palm. **D**) Resources collected from S7 entering Sainte Luce. **E**) Slash and burn (tavy) in the north of fragment S8. **F**) The effects of fire in the southern area of S9. **G**) *Tenrec ecaudatus* killed for bushmeat in S9. **H**) *Eulemur collaris* female with snare attached to hand in the protected forest S9. **I)** *Coua gigas* on release after being captured in a snare in S9. **J**) A Critically Endangered *Dermochelys coriacea* captured by fishermen in Manafiafy. The animal was later purchased and released by a local eco-lodge. **K**) A skewer inside a tree hollow, used to detect and extract nocturnal lemurs. **L**) An aerial view of the QMM/RioTinto mine at Mandena (Google images).

The two other invasive insectivorous species present in Sainte Luce, *Suncus murinus* and *Suncus etruscus* are both relatively uncommon. Generally considered a human commensal (Garbutt, 2007), *S. murinus* has been encountered in core areas of S9, although it is again not considered a direct competitor with endemic tenrec species (Goodman and Rakotondravony, 2000). The origin of *S. etruscus* in Madagascar is debated (Hutterer, 1993; Garbutt, 2007), however represents a voracious predator of invertebrates. Both may reduce prey for endemic species. Of the avifauna, the Common Mynah (*Acridotheres tristis*) has established a permanent breeding presence in Sainte Luce in recent decades, particularly in fragment S8. Whilst abundant in exotic plantations across Sainte Luce, it remains absent from the other forests. It is thought that its presence could be linked with a decline of native forest species (Ellis, 2003). Near villages and forest edges, domestic animals pose a further noteworthy threat. Cats are not abundant in Sainte Luce but are often kept by shopkeepers to control rodent populations. In Sainte Luce, cats have been observed predating nocturnal lemurs (*Cheirogaleus thomasi*), rodents (*Rattus rattus*), snakes (*Liophidium torquatum* and *Thamnosophis lateralis*), chameleons (*Furcifer lateralis* and *Furcifer oustaleti*), skinks (*Trachylepis gravenhorsti*) and assorted invertebrates (*Anostostomatidae* spp., *Blaberidae* spp. (S. Hyde Roberts. pers. obs). Cats do not typically enter the forest, but one cat was observed several hundred metres inside the protected forest S9, two metres high in a tree (E. Račevska. pers comm). In Sainte Luce, dogs are uncommon and considered as taboo or 'fady' by the majority of the community. However, a small number of dogs are kept for security and for hunting tenrecs. The impact of dogs on natural carnivore populations is unclear.

Current status (new species and taxonomic updates).

Since the early floral and faunal studies in the early 1990's (Lowry and Faber-Langoen, 1991; Lewis Environmental Consultants, 1992b), a remarkable revolution in molecular biology has led to the development of new genetic tools and an unprecedented ability to explore phylogenetic relationships. As a consequence, the identity of many species formerly identified based on general morphological characters can now be re-evaluated and their conservation status updated. Many of the species confirmations presented herein are based on works, largely conducted by SHR over the past six years and many remain unpublished. Whilst a full assessment of the botanical community is beyond the scope of this appraisal, it is possible to review the majority of vertebrate groups present in the area and re-examine a small number of invertebrate groups. Comprehensive species lists and IUCN Red List classifications are provided in the **Appendix** (**Table 6a–6e**).

Invertebrates

Only a small number of invertebrate taxa have been well studied within the Sainte Luce area to date; Coleoptera; Diplopoda, Odonata, Lepidoptera, Mantodea and Phasmatodea (Wesner and Wägele, 2007; Schütte, 2007; Schütte and Razafindraibe, 2007; Hyde Roberts unpub. data) and further work is urgently required. The terrestrial invertebrate fauna appears to be particularly rich, containing many new undescribed forms. Sainte Luce is known to support a unique and highly diverse community of Spirobolida millipedes and the most speciose community of Sphaerotheriida millipedes within the southeastern littoral zone (Wesner and Wägele, 2007). Furthermore, the community contains a number of micro-endemic forms which are restricted to forest interiors and do not tolerate plantations or open areas (Wesner and Wägele, 2007). Based on the work of Schütte (2007), Sainte Luce also supports the greatest diversity of Mantodea and Phasmatodea species in the littoral forests of the southeast, and both groups similarly encompass a large number of undescribed forms (Schütte, 2007). Work to assess the diversity of the Coleopteran community is currently underway, following a significant collection made in 2016 (SEED Madagascar, unpub. data).

The flying invertebrate taxa Odonata and Lepidoptera are more cosmopolitan but include a number of important taxa. Schütte and Razafindraibe (2007) reported 26 species of dragonfly and damselfly from his study of the fauna in Sainte Luce, including an undescribed Gomphiid species (*Isomma* sp. nov). Since 2015, a further eleven species have been observed in the area (SEED Madagascar unpub. data), including the notable re-discovery of a species missing since 1907; *Libellulosoma minutum* (Hyde Roberts et al, 2019). The community contains seven Data Deficient and two Endangered species (*Acisoma cf. ascalaphoides* and *Teinobasis alluaudi*) with some species restricted to forest habitats and others requiring specific aquatic conditions to reproduce (Schütte and Razafindraibe, 2007). The butterfly community of Sainte Luce so far stands at 56 confirmed species, with the majority widespread across Madagascar (Hyde Roberts unpub. data). There does not appear to be any butterfly species restricted to the littoral habitats, however additional species are likely to be added with increased surveying effort. Very few butterfly species are currently assessed by the IUCN.

Amphibians and reptiles

By far the greatest number of taxonomic amendments and changes have taken place within this group. Prior to 2015 all work carried out on the herpetofauna of Sainte Luce was based solely on morphological examination. The species inventory provided by the initial EIA (Lewis Environmental Consultants, 1992b) was greatly developed by Ramanamanjato (2006) and the

number of observed species in the area leapt from 55 to 69. However, given that many of the families within the group are characterised by high levels of cryptic diversity, ongoing species discovery and regular taxonomic revision, a definitive appraisal was required to properly assess local threats. A community wide barcoding project was initiated in 2015 (SHR unpub. data) with the aim of definitively identifying all species and providing a reliable foundation for future conservation efforts. Genetic tools helped resolve a number of identification problems and has led to a large number of species corrections, new records and the identification of novel candidate species. Based on an assessment of previous works and new genetic evidence, the number of amphibian species inhabiting Sainte Luce is 22. This is down one from the list provided by Ramanamanjato (2006), however the record of *Madecassophryne truebae* is highly dubious. Included in the revised figure are seven candidate new species, three taxonomic revisions (Bellati et al, 2018) and two new area records (*Boophis sp. aff. Pauliani* and *Boophis sp. aff. picturatus*). The large number of *Mantidactylus* species that appear in previous inventories appears to be a case of mistaken identity based on unvalidated species characters and taxonomic inflation associated with the difficulties of identifying cryptic species. New candidate species occur within the genera *Bommersia*, *Boophis*, *Guibemantis*, and *Mantidactylus*. In addition, examination of the eastern miniaturised Microhylid frogs (formerly *Stumpffia*), including specimens from Sainte Luce, has resulted in the formation of a new Genus; *Mini* (Scherz et al, 2019). The validated amphibian community includes one Critically Endangered species (*Guibemantis diphonus*), three Endangered species (*Anodonthyla nigrigularis*, *Guibemantis annulatus* and *Guibemantis wattersoni*), a single Near Threatened species (*Gephyromantis leucocephalus*), nine are considered as Least Concern and a further eight species are not yet formally described or assessed.

The reptile fauna proved similarly in need of review, with ten new candidate species identified (across the families Chamaleonidae, Gekkonidae, Lamprophiidae and Scincidae), four new records for the area (*Pelomedusa subrufa*, *Dermochelys coriacea*, *Liophidium vaillanti* and *Indotyphlops braminus*) and four species corrections. The total number of reptiles now confirmed in Sainte Luce is 52, up from 46, however other plausible records from older studies if confirmed could raise the figure to as high as 55. Of the confirmed species, three are considered as Critically Endangered (*Dermocheyls coriacea*, *Eretmochelys imbricata*, *Phelsuma antanosy*), two are Endangered (*Chelonia mydas* and *Liophidium kely*), four are Vulnerable (*Caretta caretta*, *Pseudoxyrhopus sokosoko*, *Zonosaurus anelanelany* and *Zonosaurus maximus*), one species is Data Deficient (*Matoatoa* cf. *spannringi*) whilst 30 are Least Concern and a further ten are Not Assessed as they represent candidate new species. The amphibian and reptile community of Sainte Luce is similar in many respects to that of the eastern humid forests and includes a large

proportion of forest dependent species with specific habitat specialisations. The majority of species also possess little capacity for natural dispersal between isolated forests, and fragments larger than 300ha appear necessary to support levels of present levels of biodiversity (Ramanamanjato, 2006).

Birds

To date there have been five major bird studies conducted in Sainte Luce, including both the initial mining assessment (Lewis Environmental Consultants, 1992b) and the ongoing work of SHR since 2014 (unpub. data) (Goodman et al, 1997; Ellis, 2003; Watson et al, 2005). Broadly each study has aimed to compile an accurate species inventory for the area, although different methods have been adopted (e.g. season, survey duration and habitat focus has varied). However, the combined results offer an insight into the diversity of species using the landscape and importance of habitat heterogeneity for supporting avian biodiversity. When the observational records from each study are compiled and adjusted for taxonomic changes, a total of 117 species have been recorded in Sainte Luce, although many appear rare. Given birds capacity for dispersal, it is perhaps no surprise that different studies have produced disparate inventories and total richness estimates. Whilst a number of observations seem anomalous, and many species have not been seen in the most recent studies, they cannot be discounted. Of the 117 species across the five studies, 36 species may be considered as forest dependent, 23 as preferring open areas, 24 are known to utilise a mixture of both forest and open areas, 24 species are associated with aquatic habitats and ten with coastal environments. 41% of species are endemic to Madagascar, but none are endemic solely to littoral forests (Goodman et al, 1993; Watson et al, 2005). However, it has been noted that the littoral forests contain a unique avian assemblage, and that littoral forests provide important links between spiny and humid forests (Watson et al, 2005). When all records are considered only a single species, Meller's duck (*Anas melleri*) is classified as Endangered, four are considered Vulnerable (*Charadrius thoracius*, *Falco concolor*, *Gallinago macrodactyla* and *Glareola ocularis*), three Near Threatened (*Accipiter henstii*, *Accipiter madagascariensis* and *Lophotibis cristata*) and 107 are Least Concern. A further two species remain unclassified by the IUCN as their taxonomic status remains unresolved.

Small mammals, carnivores and bush pigs

At present, the small mammal community consists of three tenrec species (*Tenrec ecaudatus*, *Setifer setosus* and *Oryzorictes hova*), two rodent species (*Rattus rattus* and *Eliurus webbi*) and two insectivores (*Suncus murinus* and *Suncus etruscus*). The identity of each of these species is now genetically confirmed (SHR unpub. data) and amends earlier misidentifications, with

Microgale pusilla presumably mistaken for *S. etrucus* (Lewis Environmental Consultants, 1992b). The number of Tenrecidae species remains unchanged (three) with the additional record of *O. hova* in fragment S9 (SHR unpub. data). The distribution of these species across the fragmented landscape needs further investigation but no tenrecs were detected in pitfall traps (SHR unpub. data) in the smaller protected fragment S8. All species are currently considered as Least Concern by the IUCN. The carnivore fauna appears to consist of a single species, the Malagasy civet (*Fossa fossana*), which has been observed briefly on a number of occasions at night in cassava plantations near to forest edges and has been captured by camera trap inside the largest protected fragment S9 (E. Račevska. pers. comm). Whilst the species has a relatively large eastern distribution, it is thought to rely on intact forest and is considered largely intolerant of fragmented habitats (Gerber et al, 2012; Hawkins, 2015). Habitat loss and hunting are cited as the primary threats to this Vulnerable species (Hawkins, 2015). Evidence for the return of the bushpig (*Potamochoerus larvatus hova*) has been observed in the past 18 months in the north of forest fragment S9. Local guides attribute the return down to a large fire in 2019, driving the pigs towards Sainte Luce. Before this, bushpigs had been absent from the area for decades after a prolonged period of effective hunting (H. Longosoa. pers. comm). The ecological impact of bush pigs in small protected fragments is unknown.

Bats

The Madagascar flying fox (*Pteropus rufus*) is recognised as a key seed dispersal agent in the Sainte Luce, able to carry and deposit seeds over large areas and between fragments (Bollen, 2002; Bollen and Donati, 2006; Gérard et al, 2015; Hyde Roberts et al, 2016). The need to protect the roost site in S6 was highlighted in the initial review (Bollen and Donati, 2006), but the fragment is now experiencing heavy logging pressure as a community use zone, and also exists within the mining footprint. Despite this, conservation initiatives led by SEED Madagascar have resulted in quasi local protection, and the colony appears to have initially rebounded rapidly, rising from around 160 individuals in 2015 to approximately 400 today (S. Hyde Roberts. pers. obs). However regular disturbance and logging near to the roost site continues. The species has recently been highlighted as a major conservation priority, with a call to reassess its conservation status (Brook et al., 2019). The microbat community in Sainte Luce requires urgent review. A study conducted by Jenkins et al (2007) as part of the ecological assessment by the mine recorded nine - ten species by means of mist netting and acoustic detection. Of those identified, *Hipposideros commersoni* is considered as Near Threatened (Monadjem et al, 2020). Intriguingly, the study reported an unknown vespertilionidae species and a further hipposiderid species whose

vocalisations were unknown (Jenkins et al, 2007). Further species are known to inhabit nearby areas and additional survey effort may increase the species inventory for Sainte Luce.

Lemurs

Perhaps the most important taxonomic changes have occurred within the lemur community, with all four species under-going revision since the initial environmental impact studies (Lewis Environmental Consultants, 1992b; Groves, 2001; Zaramody et al, 2006; Rasoloarison et al, 2013; Lei et al, 2014). All three nocturnal species were described from cryptic species complexes whilst *Eulemur collaris* was promoted to full species status from earlier being recognised as a subspecies of *Eulemur fulvus*. The genetically validated community of lemurs present in Sainte Luce now comprises of one Lemuridae species, *E. collaris*, one Indriidae, *Avahi meridionalis* and two Cheirogaleid species, *Cheirogaleus thomasi* and *Microcebus tanosi*. These revisions have direct implications and consequences for conservation and biodiversity management. All four lemur species are now classified as Endangered by the IUCN (Donati et al, 2020b; 2020c; 2020d; Ganzhorn et al, 2020). The three nocturnal lemurs appear to be present in all remaining fragments, whilst *E. collaris* occupies S1, S2, S8, S9 and S12 (Hyde Roberts et al, 2020) and a patch of sacred forest near Manafiafy.

Missing species / Impacts on local biodiversity

Since biodiversity assessments first began in Sainte Luce three decades ago, a number of important species appear to have vanished from the area (**Table 28**). Whilst it is plausible that some smaller, rare and cryptic species could go undetected for prolonged periods (e.g. the pandanusicollid frog *Guibemantis cf. pulcher* and the fossorial skink *Flexiseps cf. macrocercus*), larger more conspicuous species (e.g. the fossa *Cryptoprocta ferox* and the southern lesser bamboo lemur *Hapalemur meridionalis*) would almost certainly have been detected given the consistent level of research effort in the main forest fragments. Given that the majority of research in recent years has been focused on the protected fragments S8 and S9 and the community use forests S6 and S7, it is also possible that some species persist within the wider mosaic of fragments (e.g. the plated lizard *Zonosaurus anelanelany* was described from S17 but remains unknown from other fragments). However, many of the more remote fragments are smaller in size, highly degraded and are considered unlikely to support viable populations of rare forest dependent species. The loss of larger vertebrate species, and particularly predatory species from the protected

areas is a real concern and may ultimately impact future ecosystem functioning and exacerbate the effects of forest fragmentation (Terborgh et al, 2001; Estes et al, 2011; Colman et al, 2014).

Whilst it is difficult to diagnose the disappearance of many species, the loss of the larger and more specialist taxa may represent the losses forecast by earlier studies, anticipating the effects of fragmentation and forest degradation (Ganzhorn et al, 2001; Bollen and Donati, 2006). For example, carnivores such as *Cryptoprocta ferox* are considered to be particularly vulnerable to such effects, persisting at low density and requiring large territories (Hawkins and Racey, 2005). However, the loss of particular species may be partly explicable by circumstantial evidence. The disappearance of *Hapalemur meridionalis* appears to have coincided with the large-scale reduction of forest fragment S8 in the early 2000's, with the last credible sighting of the lemur made in 2003 (Ellis, 2003). Although, focused surveys in 1999 failed to observe the species and concluded that the species was either already extirpated or existed at very low density (G. Donati. pers. comm). The loss of important food resources may have impacted the species, however the hunting of lemurs for bushmeat was also prevalent at the time and may have catalysed any extirpation (L. Johnarson. pers. comm). In contrast, the absence of *Cheirogaleus major* is puzzling as the species is still present in smaller and less intact littoral forest further south (Mandena), and in the humid Vohimena mountains to the west. In this instance, confusion with the similar and abundant *Cheirogaleus thomasi* must be considered as a possibility. Of the avifauna, a total of 35 bird species recorded in previous studies have not been detected since 2010. Whilst many bird species may only rarely visit Sainte Luce, Meller's duck (*Anas melleri*) was considered a resident in the area in the early 2000's, but under threat from the local community who hunt aquatic birds (Ellis, 2003). Its disappearance is a concern.

The loss of species provides a stark reminder of the on-going threats facing littoral ecosystems and the conservation challenges ahead. It is now evident that even the largest littoral forest fragments in Sainte Luce cannot support a truly natural vertebrate community and the loss of important species will profoundly affect ecosystem dynamics. The losses also highlight the necessity to preserve functional habitat connectivity to facilitate species movement. Furthermore, whilst this list deals largely with the more obvious vertebrate taxa, the impact of the combined threats on the invertebrate and botanical communities needs further attention. Baseline inventory work is becoming ever more urgent in order to assess future biodiversity losses. Furthermore, it has long been known that important botanical resources are under great pressure (Lowry and Faber-Langdoen, 1991; Hogg et al, 2013) and some utilitarian species (e.g. *Calophyllum pervillei*) may have already been lost from the area.

Table 28.

Species not observed in Sainte Luce over the past ten years. Bird species are restricted to forest dependent species and the Endangered *Anas melleri*.

Order	Family	Species	Common Name	Status	Last Record
Primates	Lemuridae	*Hapalemur meridionalis*	Eastern Bamboo lemur	VU	Azafady, 2003 - S8
	Cheirogaleidae	*Cheirogaleus major*	Greater Dwarf Lemur	DD	Ganzhorn et al, 2008
Carnivora	Eupleridae	*Cryptoprocta ferox*	Fossa	VU	Lewis Environmental Consultants, 1992
		Galidia elegans	Ring-tailed vontsira	LC	Lewis Environmental Consultants, 1992
Aves	Accipiter	*Accipiter henstii*	Henst's Goshawk	NT	Watson et al, 2007
		Aviceda madagascariensis	Madagascar Cuckoo-hawk	LC	Watson et al, 2007
	Anatidae	*Anas melleri*	Meller's Duck	EN	Azafady, 2003
	Cuculidae	*Coua reynaudii*	Red-fronted Coua	LC	Watson et al, 2007
	Falconidae	*Falco concolor*	Sooty Falcon	VU	Watson et al, 2007
		Falco eleonorae	Eleonora's Falcon	LC	Azafady, 2003
	Vangaidae	*Cyanolanius madagascarinus*	Blue Vanga	LC	Watson et al, 2007
		Leptopterus chabert	Chabert's Vanga	LC	Watson et al, 2007
		Schetba rufa	Rufous Vanga	LC	Watson et al, 2007
Squamata	Lamprophiidae	*Leioheterodon modestus*		LC	Ramanamanjato, 2008
		Micropisthodon ochraceus		LC	Last observed 2010 - S8
	Scincidae	*Flexiseps* cf. *macrocercus*	Black-striped Skink	LC	Ramanamanjato, 2008
	Mantellidae	*Guibemantis* cf. *pulcher*			Ramanamanjato, 2008

Key species / Seed dispersers / Conservation actions

Zoochory and the importance of conserving key frugivore – plant interactions were specifically highlighted in the previous review (Bollen and Donati, 2006) and remain a key priority. It is clear that several species in Sainte Luce consume fruit and facilitate seed dispersal (Bollen et al, 2004; Lahann, 2007; Račevska et al, 2020) and that the preservation of functional relationships is vital for maintaining complex forest communities (Fleming et al, 1987). The need to conserve frugivorous species in Madagascar is made greater by the realisation that many large bodied seed dispersers have become extinct in relatively recent times, potentially disrupting dispersal mechanisms (Godfrey et al, 2004; Mittermeier et al, 2010; Goodman and Jungers, 2014). Today the community of animal seed dispersers in Sainte Luce comprises of lemurs (*Eulemur collaris*, *Cheirogaleus thomasi* and *Microcebus tanosi*), bats (*Pteropus rufus*), rodents (*Eliurus webbi* and *Rattus rattus*), birds (*Alectroenas madagascariensis*, *Coracopsis nigra*, *Coracopsis vasa*, *Coua gigas*, *Hypsipetes madagascariensis*, *Streptopelia picturata* and *Treron australis*) and potentially some reptiles (*Zonosaurus* spp.), however the utility of each species varies greatly in its contribution to ecosystem function (Bollen and Donati, 2006). Although there appears to be notable overlap in fruit predation between species (Bollen, 2002), some (e.g. fruit bats, fruit pigeons and parrots) are better able to disperse seeds across a fragmented landscape. Whilst many

frugivorous bird species are not as abundant in Sainte Luce as elsewhere and some are uncommon (S. Hyde Roberts. pers. obs), most long-distance seed dispersers presumably visit all forest fragments in Sainte Luce. However long-distance dispersal also increases the risk of introducing unwanted invasive species (e.g. *Psidium cattleianum*) into Sainte Luce (Picot et al, 2007; Kull et al, 2014; DeSisto et al, 2020). In contrast, the capacity for non-flying species to disperse seeds is largely restricted by forest fragmentation.

At present, *Eulemur collaris* is the only species known to be able to disperse large seeds (Ganzhorn et al, 1999; Bollen et al, 2004), leaving tree species with larger seeds limited means to propagate between fragments. Facilitated restoration of protected forests should consider including cultivated tree species whose seeds are too large to be naturally dispersed by extant animals (Ingle, 2003; Bollen and Donati, 2006). In confined forests, the preferential hunting of frugivorous species poses a substantial threat to both animal populations and forest dynamics (Wallace and Painter, 2002). Larger frugivorous species are also known to be particularly vulnerable to the detrimental effects of habitat fragmentation and degradation due to food patchiness and seasonal fluctuations (Johns and Skorupa, 1987; Eppley et al, 2020). However, the development of a local *dina*, which formalised local customs and set out a framework for the enforcement of local laws and prohibitions in 2000-2001 seems to have reduced the level of hunting (Bollen and Donati, 2006; Rarivoson, 2007). Simultaneously, the continuous presence of international researchers in Sainte Luce from 1999 onwards, along with a regular environmental educational programme appears to have ameliorated hunting pressure. The trend appears to be reflected in the population of *E. collaris*. Although a new census is urgently needed, anecdotally the population seems to have increased over the past decade. Similarly, groups are now re-colonising fragments where they had long since been extirpated (Ganzhorn et al, 2008; Nguyen and Donati, 2012; Hyde Roberts et al, 2020), although the drivers behind these range expansions remain unclear.

In line with recommendations made in the earlier review (Bollen and Donati, 2006), a number of local conservation interventions have been implemented by SEED Madagascar in order to prioritise ecologically important frugivorous species and functional ecological relationships. The quasi protection of the *Pteropus rufus* roost site in S6 has seen a rapid increase in colony size, with the number of bats increasing by 150% over a four-year period (S. Hyde Roberts. pers. obs). The community agreed establishment of a no-logging area encompassing 38ha of forest, alongside a community-based education program has reduced roost disturbance and appears to have ultimately benefitted the colony. The scheme also funds local resource management bodies

through income generated through ecotourism, as ecolodge guests and researchers pay a small fee to visit the colony. The holistic program has so far proven an effective strategy for increasing colony size. However, the long-term protection of the roost remains uncertain as despite the protection of the roost site being codified into local dina, logging still occurs close to the roost and the broader environmental program of QMM is likely to supersede local protections.

A further initiative to reconnect isolated forest patches in the protected fragment S8 is also now underway. A series of four forest remnants, isolated during the early 2000's, are currently being linked by the creation of a series of short habitat corridors. Habitat corridors are becoming an increasingly important tool for conservation biologists, facilitating animal and plant dispersal and increasing the population viability of small vulnerable populations (Bennett, 1990; Brooker et al, 1999; Haddad et al, 2003; Gilbert-Norton et al, 2010; Andriamandimbiarisoa et al, 2015). The project, developed by SHR and SEED Madagascar aims to reunite nocturnal lemur sub-populations, consolidate over 30ha of disconnected forest patches and link them to the main body of protected fragment S8. Ultimately the work will increase the size of connected forest from 40ha to over 70ha. Furthermore, the project is considered a pilot and a means of assessing the future feasibility of connecting more distantly isolated forests. The creation of corridors has long been considered a priority for the area (Ganzhorn et al, 1997, Bollen and Donati, 2006) as natural forest regeneration is slow (Lowry and Faber-Landoen, 1991; Ganzhorn et al, 1997; Vincelette et al, 2007) and fire prevention policy and agricultural encroachment prevents natural expansion. Whilst some species appear initially reticent to utilise corridors initially (Chapman and Peres, 2001), it is expected that once established, corridors will facilitate the dispersal of vulnerable species. Given the expected loss of existing forest in years to come, expanding protected forests is vital for securing biodiversity and ecological function long-term.

A variety of additional conservation actions are currently underway in Sainte Luce, developed by a range of local stakeholders and largely aiming to protect important economic and cultural resources. Projects range from small-scale species-specific projects such as the cultivation and transplantation of threatened palms (e.g. *Dypsis saintelucei*, *Dypsis brevicaulis* and *Beccariophoenix madagascariensis*), to a large-scale sustainable fisheries project working to protect marine resources and local livelihoods (Project Oratsimba is a collaboration between SEED Madagascar and the Indian Ocean Commission). Ancillary projects have also been developed in parallel in an attempt to increase the availability of important fisheries related materials, particularly those used in the construction of lobster traps (e.g. *Dypsis scottiana*, *Flagellaria indica* and *Bambusa multiplex*).

Conservation recommendations

A number of practical interventions and conservation measures must be developed to address the threats and counteract the expected loss of forest cover over the coming decades (Bollen and Donati, 2006; Ganzhorn et al, 2007; Temple et al, 2012). Now that both the protected areas and forests within the mining footprint are established (Vincelette et al, 2007; Temple et al, 2012), solutions are urgently needed to mitigate the impact of the combined threats and minimise the loss of further species. A number of local studies have concluded that smaller littoral forest fragments are less effective for maintaining biodiversity than large fragments and forests below a minimum size are unlikely to sustain current levels of vertebrate diversity (Ganzhorn, 2000; Watson, 2005; Ganzhorn et al, 2007; Ramanamanjato, 2007). Minimum forest size requirements vary between vertebrate groups but estimates of between 200-300ha appear necessary for lemurs, amphibians, reptiles and birds (Ganzhorn et al, 2007; Ramanamanjato, 2007, Watson et al, 2007), with patches as large as 1000ha necessary to safeguard viable vertebrate assemblages long-term (Ganzhorn et al, 2000). Under current projections the largest remaining forest blocks will be S9 and S17 at 190ha and 237ha respectively (QMM, 2001). It is therefore evident that the existing protected forests require expansion and improved connectivity. However, there is limited opportunity to expand either fragment in the foreseeable future as S9 is largely enveloped by the proposed mining zone, and S17 is bordered by the coastline and the exploitation zone (Temple et al, 2012 and see **Fig. 32**). The smaller protected forest S8 is therefore a priority area for reforestation and restoration projects. Furthermore, the successful restoration of the heavily degraded southern fragments S1 and S2, proposed by QMM, will be vital in the long-term recovery of the Sainte Luce ecosystem.

Mitigating the loss of animals once mining operations commence will be a major priority. The rapid clearance and modification of forested and aquatic habitats will necessitate the movement of myriad animals and poses a substantial conservation problem. Whilst most flying taxa (some species are conservative or poor flyers) will be able to autonomously relocate, a strategy to minimise the loss of forest dependent terrestrial species must be developed. In Mandena, a series of habitat corridors were established in order to facilitate animal movement between forests ahead of the mine dredge (G. Donati. pers. comm.), however this technique is not feasible in Sainte Luce given the isolation of fragments and the difficult terrain. It is apparent that any strategy to minimise the impact of forest clearance must consider all available conservation tools, utilising translocation techniques, corridors, ex-situ captive breeding and reintroduction programmes along with extensive pre- and post-mining population monitoring. Future translocation work may

utilise the experience gained from the relocation of *Eulemur collaris* in Mandena, which although revealed many associated pitfalls, was largely positive and demonstrated that even large animals are able to adequately adapt (Donati et al, 2007; 2020). However, given that littoral assemblages contain many habitat specialists and species that require specific niches (e.g. *Guibemantis* spp. and *Phelsuma antanosy*), simply moving large numbers of animals from the mining fragments to protected fragments will be problematic and could unbalance ecological relationships.

The supply of natural resources currently derived from the littoral forests for fuel and construction by the community needs to be alternatively sourced in coming years and establishing sustainable community use forests is now perhaps the most important objective for the area. Whilst some small-scale plantations, comprised of fast-growing introduced species (e.g. *Acacia mangium*, *Eucalyptus citriodora*, *Eucalyptus robusta*, *Grevillea robusta*) have been planted over the past decade by various stakeholders (QMM, FIMPIA, SEED Madagascar) and are already maturing in Sainte Luce, reforestation initiatives need to be scaled up in coming years if community needs are to be met. Similarly, some sustainability mechanism needs to be introduced into the forest management strategy. In the short-term, an appraisal of reforestation efforts to date and the status of the existing plantations needs to be completed as a priority, in order to fully discern the magnitude of work still required. Whilst plantation habitats are known to provide important refuge for many animal species globally (Brockerhoff et al, 2008) and appear to have benefited some lemur species (Ganzhorn, 1987; Ganzhorn et al, 1991; Eppley et al, 2015; 2017 and see **Chapter 6**), they generally support an impoverished biodiversity, largely comprised of adaptable and widespread species (Armstrong and van Hensbergen, 1996; Moore and Allen, 1999; Ramanamanjato and Ganzhorn, 2001; Lindenmayer and Hobbs, 2004; Watson, 2005; Wesener and Wägele, 2007; Liu et al, 2016; Braun et al, 2017). As a result, plantations should not be considered as a total substitute for natural littoral forest and initiatives to expand natural standing forest must be explored in parallel (Barlow et al, 2007; Watson et al, 2018). Furthermore, local community members largely favour traditional endemic species for many purposes (e.g. medicine, ceremony, livelihoods) (QMM, 2001; Vincelette et al, 2006; 2007d). In the long-term however, largescale community forests consisting of non-native tree species can provide a vital role in preserving littoral forest biodiversity, reducing pressure on threatened species and natural forest resources, as well as reducing rates of forest loss and degradation.

The placement of plantations is also mooted, with some recommending plantations should be positioned adjacent to existing forests (Bollen and Donati, 2006), however there is contrary evidence suggesting that plantations support a greater abundance of invasive species

(Ramanamanjato and Ganzhorn, 2001; Lantschner et al, 2012; Silmi et al, 2013) which could then further permeate natural forests. Furthermore, linking plantations to protected forests could blunt the effectiveness of established protective measures. Whilst certain studies indicate that some non-native species (e.g. *Acacia mangium*) can initially improve soil quality and accelerate forest succession (Corlett and Hau 2000), evidence from mixed plantations suggests that non-native species can restrict the natural succession of endemic species through nutrient competition, impacting both growth and overall survival rates (Vincelette et al, 2007d). Furthermore, certain commonly used species (e.g. *Eucalyptus* spp.) are known to exude natural pesticides which may reduce invertebrate diversity around edge habitats. As a result, the positioning of community use plantation forests must be carefully considered as the remaining protected forests will be vulnerable post mining. Similarly, the creation of a new 225ha forest (part of QMM's restoration commitment), originating from recovered topsoil and its preserved seed layer (Temple et al, 2012) must be positioned carefully to facilitate future connectivity between protected fragments whilst simultaneously enabling colonisation by animal communities.

Fires remain a considerable threat to standing forest and to any future restorative projects. Fire has destroyed a number of small plantations in Sainte Luce (L. Bass. pers. comm) and habitat corridors and small forest fragments in Mandena in the past (Bollen and Donati, 2006). Particular care must be taken by any corridor project, as corridors are known to also propagate fire in some circumstances (Brudvig et al, 2012). At present, the developing habitat corridors in Sainte Luce are bordered by firebreaks. The current protective measures taken by COBA and FIMPIA, supported by QMM, to clear ten metre firebreaks around protected forests biannually should be reviewed. It may be possible to maintain firebreak effectiveness and enable natural forest succession by extending the firebreak out several metres each iteration. Although there is no known precedent, the adjustment could provide a cost-effective alternative to laborious restoration, enabling forests to rapidly expand and could be particularly useful in fragment S8. Although unprotected fires are prohibited under local community law (dina), further community education by local stakeholders could add additional value. The situation is similar with both hunting and agricultural expansion. Agricultural plots are highly visible, and if created illegally, breaching local dina, local authorities theoretically should be capable of issuing relevant sanction based on the dina. However, the familial and close-knit nature of community life often forestalls prosecution. Therefore, capacity building with the aim of strengthening local enforcement bodies and deterring prohibited activities should be fostered. Similarly, the decline in hunting over the past two decades represents a success for both the effectiveness of community laws and local education programmes. However, there is no guarantee that current levels will continue, and

regular reinforcement should be encouraged alongside community education on the impacts of hunting on wildlife populations. A formal monitoring and reporting system should be adopted by local forest police patrols and all prohibited acts should be systematically recorded. Not only would this provide evidence for local enforcement but would also provide much needed data on hunting and illegal logging in the area.

Beyond the broader protection of the forest fragments, a number of threatened species require specific interventions. A list of 21 prospective priority species for Sainte Luce is presented in **Table 29** along with a list of twelve priority forest dependent vertebrate species in **Table 30** (and see **Fig. 34**). The species that populate each list are selected based on a number of criteria, including current IUCN classifications, known distributions and local abundance, ecological utility (i.e. seed dispersers, pollinators, trophic importance) and economic or functional importance to the local community. Whilst there are many undescribed and threatened species in the littoral forests of Sainte Luce, the listed species provide a selection of species that require urgent attention and should form the basis of any future Conservation Action Plan.

Table 29.

A list of 21 priority species in Sainte Luce. IUCN classifications as of December 2020. *Indicates that the taxonomic status of the species remains unconfirmed. The list does not include species listed in **Table. 28,** however species from that list should also be considered as high priorities if re-discovered.

Species	Common or Vernacular Name	Primary Reason	IUCN Status
Eulemur collaris	Red-collared brown lemur	Ecological / Conservation	EN
Phelsuma antanosy		Conservation	CR
Avahi meridionalis	Southern woolly lemur	Conservation	EN
Dypsis saintelucei	Telopoloambilany	Conservation / Utilitarian	EN
Microcebus tanosi	Anosy mouse lemur	Ecological / Conservation	EN
Cheirogaleus thomasi	Thomas' dwarf lemur	Conservation	EN
Pteropus rufus	Madagascan flying fox	Ecological / Conservation	VU
Fossa fossana	Malagasy civet	Ecological	VU
Dypsis brevicaulis		Conservation	CR
Calophyllum pervillei	Vitano	Utilitarian / Conservation	NA
Liophidium kely		Conservation	EN
Caretta caretta	Loggerhead sea turtle	Conservation	VU
Matoatoa cf. *spannringi*		Conservation	DD*
Guibemantis diphonus		Conservation	CR
Eugenia cloiselii	Ropasy / Rotra	Utilitarian	EN
Dypsis scottiana	Raotry / Amboza	Utilitarian / Conservation	VU
Libellulosoma minutum		Conservation	DD
Panulirus homarus		Economic / Conservation	LC
Flagellaria indica	Vahimainty	Utilitarian / Conservation	NA
Anodonthyla nigrigularis	Black-throated climbing frog	Conservation	EN
Lepironia mucronata	Mahampy	Economic / Ecological / Utilitarian	NA

Table 30.

Twelve priority forest-dependent vertebrate species in Sainte Luce. IUCN classifications are current as of December 2020. *Indicates that the taxonomic status of the species remains unconfirmed. The list does not include species listed in **Table. 28** and species from that list should also be considered priority species if re-discovered.

Species	Common or Vernacular Name	Primary Reason	IUCN Status
Eulemur collaris	Red-collared brown lemur	Ecological / Conservation	EN
Phelsuma antanosy		Conservation	CR
Avahi meridionalis	Southern woolly lemur	Conservation	EN
Microcebus tanosi	Anosy mouse lemur	Ecological / Conservation	EN
Cheirogaleus thomasi	Thomas' dwarf lemur	Conservation	EN
Pteropus rufus	Madagascan flying fox	Ecological / Conservation	VU
Fossa fossana	Malagasy civet	Ecological	VU
Liophidium kely		Conservation	EN
Matoatoa cf. spannringi		Conservation	DD*
Guibemantis diphonus		Conservation	CR
Anodonthyla nigrigularis	Black-throated climbing frog	Conservation	EN
Palleon sp. nov		Conservation	NA

The original shortlist of priority species recognised by QMM in an early Biodiversity Action Plan (BAP) (reproduced in Temple et al, 2012) is now in urgent need of re-examination and revision. The original list includes 10 vertebrate species, 26 invertebrates and 90 plant species. Of these, the vertebrates (taxonomically adjusted) include the mouse lemur *Microcebus tanosi*, two species of bird (*Anas melleri* and *Ardea humbolti*), five amphibian species (*Guibemantis annulatus, Guibemantis wattersoni*, and *Guibemantis* cf. *pulcher, Mini scule* and *Madecassophryne truebae*) and two reptiles (*Phelsuma antanosy* and *Pseudoxyrhopus kely*). The 26 invertebrate species all belong within just three orders (Diplopoda, Mantodea and Phasmatodea) and reflect the limited amount of taxonomic work undertaken. Due to financial constraints, the number of priority species listed in the BAP has now been greatly reduced, however it is not clear which species have been omitted (QMM stakeholder meeting, 2018). Regardless, the original list required specific re-assessment in the context of conservation planning in Sainte Luce, particularly as the Madagascar heron (*A. humbolti*) has never been officially recorded in the area and Meller's duck (*A. melleri*) has not been observed since 2003. Recent taxonomic revisions also warrant reappraisal of the amphibian priority species. Whilst all three *Guibemantis* frog species are habitat specialists with limited ranges, two of the species are exceptionally abundant in the protected forests S8, S9 and S17. Furthermore, the observation of *M. truebae* is dubious given its preference for mid elevation (A. Crottini. pers. comm). Further work is required to relocate *G. cf. pulcher* as it has not been observed in the past decade but is expected to persist. *Microcebus tanosi* and the two reptile species continue to warrant priority status, with *P. antanosy* seemingly amongst the

rarest gecko species in the world. Of the priority invertebrates, little further information is available as to their current conservation status, and they should also continue to be treated as further priority species.

Figure 34 – A range of priority species in Sainte Luce. **A**) *Eulemur collaris* (female), **B**) *Avahi meridionalis*, **C**) *Cheirogaleus thomasi*, **D**) *Microcebus tanosi*, **E**) *Pteropus rufus*, **F**) *Fossa fossana*, **G**) *Phelsuma antanosy*, **H**) *Liophidium kely*, **I**) *Caretta caretta*, **J**) *Matoatoa* cf. *spannringi*, **K**) *Guibemantis diphonus*, **L**) *Anodonthyla nigrigularis*, **M**) *Dypsis saintelucei*, **N**) *Dypsis scottiana*, **O**) *Panulirus homarus*, **P**) *Lepironia mucronata*. All photographs by SHR except for **C** and **F** by Elena Račevska, **N** by John Dransfield and **O** and **P** courtesy of SEED Madagascar.

Conclusions

The littoral habitats of Sainte Luce continue to experience a number of significant threats, whilst simultaneously the biodiversity they support continues to increase in terms of both richness and importance. The total number of confirmed species has increased in nearly all major taxonomic groups (mammals from 17 to 24 recognised species, birds from 77 to 117, amphibians and reptiles from 55 to 76). Furthermore, the increases do not take into account the species that may have disappeared from the area over the past two decades, and knowledge pertaining to a number of important taxonomic groups is still entirely missing (e.g. fungi, arachnids, moths, freshwater fish). Whilst biodiversity in Sainte Luce is under serious pressure from the twin impacts of both unsustainable forest harvesting and landscape level modifications proposed by QMM, identifying and conserving key habitats (e.g. small vestiges of standing forest, connective habitats, aquatic systems) within the landscape could help to mitigate and offset long-term effects.

Given the important biodiversity that currently resides within the proposed mining footprint and the foreseeable difficulties associated with mitigating against its loss, extending the conservation zone areas to include additional important forest patches and connective habitats could provide the most prudent solution. Given the mine's commitment to preserving biodiversity (QMM, 2001) and the large amount of effort invested in to securing a positive environmental outcome (Temple et al, 2012), it would seem pertinent to review its strategy in light of these updates before operations commence. A potential means of maximising biodiversity offset could be to integrate core areas of both fragments S6 and S7 into the Conservation Zone and biodiversity offset. This would protect the important *Pteropus rufus* colony, provide local communities with a new sense of responsibility and mitigate the unsustainable resource extraction in these forests. It would further safeguard a number of priority species (e.g. *Cheirogaleus thomasi*, *Phelsuma antanosy*, *Matoatoa spannringi* and *Dypsis saintelucei*) whose principal populations exist in these areas. Besides acting as important additional reservoirs of biodiversity throughout the mining process, they could facilitate future reforestation works and act as vital connective forests post-mining.

In Madagascar as a whole, the extensive deforestation observed over the past century has been largely driven by a rapidly growing population dependent on small-scale local economies and a demand for natural resources (Gade, 1996; Casse et al, 2004; Moser, 2008). Although the level of deforestation in Sainte Luce is severe, it has been far more extensive in previous decades (notably between 2000-2010), coincident with biodiversity losses. The slow rate of overall forest cover change in Sainte Luce over the past decade suggests that mitigation and conservation

measures could effectively navigate a sustainable future for both the local communities and biodiversity. The observed change in forest cover also undermines a key tenet of the mining project; that high levels of deforestation from community usage would remove significant areas of littoral forest from within the mining zone (QMM, 2001). Whilst QMM's commitment to environmental recovery is substantial, it is clear that the recovery of littoral forests is very slow and will take many years (Vincelette, 2007). Likewise, the recovery of functional ecological assemblages may take many decades (Kumssa et al, 2004).

However, the mine promises much needed economic growth, and the creation of industrial employment could reduce local pressure on protected forests. In Mandena, protected forests have seen significant improvement over the past two decades (based on Normalized Difference Vegetation Index analysis) (Donati et al, 2020). Whilst development also brings its own environmental challenges (e.g. pollution, increased human access and roadkill), economic diversification is necessary if the community is to break its dependence on dwindling forest resources. Therefore, a compromise must be reached, maximising the benefits of local development and minimising industrial impacts on the environment and biodiversity. At the same time, eco-tourism in Sainte Luce, a highly promising local economic sector prior to the Covid-19 pandemic, must be rekindled. If biodiversity can be sustained and the community continues to benefit from its rich natural heritage, there is reason for optimism. In the meantime, the most imminent threat to biodiversity in the area emanates from the gradual loss of species from unsustainable harvesting and strategies to address these issues are urgently required. The proposed priority species lists provide an important update to help focus conservation attention in the area and since Sainte Luce appears to have already lost a number of charismatic species in recent decades, the effect of further losses serves only to diminish the areas future prospects and increases the costs associated with restoration.

CHAPTER 8

GENERAL DISCUSSION

The studies that comprise this thesis represent the first in depth investigation into the ecology, behaviour and conservation status of *Microcebus tanosi*. Each chapter provides insight into the behavioural ecology and adaptability of mouse lemurs, an ancestral primate taxon, and attempts to answer fundamental questions concerning the evolution of mouse lemur social structure and ecological adaptation. Since the initial discovery of *M. tanosi* in 2013 (Rasoloarison et al, 2013), confirming the identity of the mouse lemur species inhabiting the littoral forests of Sainte Luce became of increasing importance. Set against a backdrop of chronic habitat loss, driven by unsustainable forest resource extraction, and imperilled by proposed mining operations (QMM, 2001; Temple et al, 2012; Rio Tinto, 2017), the long-term prospects for the lemur community in Sainte Luce were unclear. Although three of the four lemur species known to occupy the study area (*Avahi meridionalis*, *Cheirogaleus thomasi* and *Eulemur collaris*) had been relatively well studied in terms of their social structures, habitat utilisation and conservation threats (Donati et al, 2007; 2011; Lahann, 2007; 2008; Ganzhorn et al, 2008; Norscia, 2008; Norscia et al, 2012), earlier attempts to research *M. tanosi* had proven difficult (J. Ganzhorn. pers. comm). As a result, many salient questions remained unanswered and demanded urgent investigation.

Studying one of the world's smallest primates using radiotracking equipment presented a considerable challenge, confounded by its highly mobile, often solitary and nocturnal habits and the dense forest setting. Furthermore, the cautionary tales of previous researchers, particularly in capturing animals, both in Sainte Luce and elsewhere across Madagascar, provided further consternation (Atsalis, 2008). However, finding solutions and overcoming these initial challenges was fundamental to pursuing the project's main research aims. Whilst confirming the identity of the mouse lemur species in Sainte Luce and increasing our understanding of species distributional patterns in the extreme southeast was important, the projects primary research aims were to investigate the adaptive nature of mouse lemur socio-ecology in the littoral forests. The project set out to explore the key environmental and social drivers behind observed behavioural patterns and to link and contextualise these derived behaviours to species conservation. Whilst mouse lemurs are generally viewed as being adaptable and somewhat tolerant of habitat disturbance, a more refined picture is now emerging whereby species-specific responses to environmental

change are recognised as being increasingly important (Rendigs et al, 2003; Lehman et al, 2006; Steffens et al, 2016; Radespiel et al, 2018).

Whilst mouse lemurs have become a powerful model species to study a wide range of biological phenomena in captivity (Radespiel and Zimmermann, 2001b; Génin and Perret, 2003; Bons et al, 2006; Hozer et al, 2019; Roberts, 2019), the majority of species remain completely unstudied in the wild. As species continue to be described (Hotaling et al, 2017; Sgarlata et al, 2019; Schüßler et al, 2020), the knowledge gap widens with regards to the natural range and expression of socio-ecological behaviours across the lineage. As such, the findings of this study facilitate greater inter-species comparisons and allow broader trends within the genus to be investigated. Furthermore, this body of work emphasises the conservation challenges and existential threats faced not only by the target species, but also by the southern littoral forests themselves and the rich biodiversity they support. This study was able to conclusively identify the mouse lemur species both in Sainte Luce and Nahampoana based on genetic evidence, rejecting the premise of sympatry with other mouse lemur species at both sites. Similarly, no evidence was found to suggest species overlap, even in habitats (Nahampoana) that could be expected to constitute contact areas with other species. However, notable differences in phenotype exist between both sub-populations and warrant further investigation.

Lemurs, like all primates are undoubtedly social animals (Jolly 1966; Kappeler and van Schaik, 2002; Ganzhorn and Kappeler, 2013) and the interaction between environmental forces and social pressures evidently results in differentiated social systems, even in closely related species. As such, the study of a species social system (a combination of social organisation, social structure and mating strategy) and the nuanced manner in which these manifest within a specific environment, can reveal important evolutionary patterns (Bearder, 1987; 1999; Kappeler, 1997). The first three chapters of this study focus on important aspects of mouse lemur evolution, i.e. morphological parameters, ranging behaviours and sleeping site ecology, factors that each reflect underlying evolutionary processes and combined define the social system of *M. tanosi*. The primary finding of these initial chapters is that the behavioural ecology and social structure of *M. tanosi* is broadly consistent with those of other studied mouse lemur species to date (Radespiel, 2000; Schwab, 2000; Weidt et al, 2004; Hending et al, 2017). Both in terms of morphology, general social structure and ecology, *M. tanosi* occupies a largely predictable mouse lemur niche, although with some key variations. This study concludes that *M. tanosi* is intermediate in morphological character compared to its congeners and shows no clear evidence for sexual dimorphism. No evidence for a latitudinal gradient amongst eastern *Microcebus* forms, in any

obvious morphological trait appears to exist, in concurrence with Louis et al (2006). However, results highlight the existence of variation between isolated sub-populations, both in terms of biometric character and phenotype, signalling a possible tendency within the genus for rapid adaptation and speciation (Hoekstra et al, 2004; Mullen and Hoekstra, 2008; Pfennig et al, 2010).

This study demonstrates that *M. tanosi*, at least within the littoral forests, conforms to the social model of a dispersed, but individualized neighbourhood system, characterised by substantial inter and intra-sexual home range overlap, akin to all other mouse lemur species studied to date (Radespiel, 2000; Lahann, 2008; Hending et al, 2017). No evidence for the spatial monopolisation of females by dominant males was found. Scramble competition appears to be the predominant reproductive strategy of *M. tanosi*, at least in wild populations, during the austral summer. During this period male individuals appear to compete for access to fertile females by occupying and patrolling large home ranges. In fact, male *M. tanosi* appear to occupy relatively large home ranges when compared to other *Microcebus* species. However, variation between studies in terms of timing means that it is not wholly clear to what extent inter-specific discrepancies are an artefact of method, or a true reflection of differentiated strategies within the genus. Yet within the relatively few species that have been assiduously studied, a small number clearly demonstrate a large degree of 'real' variation (Weidt et al, 2004; Génin, 2010).

This variation in ranging behaviour is also manifest within the strategies exhibited by each sex. Whilst home range size appears comparable between sexes during the non-breeding austral winter period in some species (*M. lehilahytsara*, *M. ravelobensis* and *M. sambiranensis*) (Randrianambinina, 2001; Weidt et al, 2004; Jürges et al, 2013; Hending et al, 2017), males of others (*M. ganzhorni* and *M. murinus*) expand their ranges during the austral summer, purportedly in search of fertile females (Pages-Feuillade, 1988; Radespiel, 2000; Lahann, 2008). In comparison, a number of studies, including this one, demonstrate that males occupy significantly larger home ranges than females during part of the year (*M. berthae* or *M. myoxinus* and *M. rufus*) (Atsalis, 2000; Schwab, 2000; Schwab and Ganzhorn, 2004; Dammhahn and Kappeler, 2005). However, this pattern is not ubiquitous. *Microcebus ravelobensis* maintain comparable inter-sexual home range sizes over the reproductive and non-reproductive seasons (Weidt et al, 2004) and conversely, female *M. griseorufus* occupy larger home ranges than male individuals in the harsh southern dry forests (Génin, 2010). Although clear patterns are emerging, further studies are required to determine the existence of any broad environmental or phylogenetic trend in reproductive strategies. Whilst the study of *M. tanosi* in Sainte Luce is extremely arduous, and

not without its ethical considerations, additional data from the non-reproductive season would facilitate a greater understanding of its social structure and a clearer idea of genus level variation. Although the littoral forests of Sainte Luce are considered largely intact relative to other examples in southeastern Madagascar, they are acutely fragmented and degraded (Green and Sussman, 1990; de Gouvenain and Silander 2003; Consiglio et al, 2006). As a consequence, it is plausible that resources are a limiting factor for *M. tanosi* sub-populations and may be impacting home range size (Campera et al, 2014). The effects, however, are likely to be more apparent in the austral winter when resources are scant (Bollen and Donati, 2005). Given that the distribution of resources and underlying productivity of a habitat, is a strong predictor for female distribution, which in turn influences male reproductive strategy and the expression of intra-sexual competition, productivity is likely responsible for driving ranging patterns in the littoral forests (Trivers, 1972; Clutton-Brock and Harvey, 1977; Emlen and Oring, 1977). In the nearby littoral forests of Mandena, a very similar habitat, the population density of *M. ganzhorni* is much higher than that of *M. tanosi* in Sainte Luce (Ganzhorn et al, 2008), yet individuals still occupy large and comparable home ranges in the austral summer (Lahann, 2008). Despite the social disparity and phylogenetic distance between the two species (Yoder et al, 2016; Hotaling et al, 2017; J. Poelstra pers. comm, 2019), the shared ranging strategies are notable. However, the malleability of ranging behaviours is poorly understood in mouse lemurs, given their broad and adaptable diets (Atsalis, 1999b).

Both *M. ganzhorni* and *M. tanosi* also utilise their similar habitats very differently, at least in terms of sleeping and nest related behaviours. Female *M. ganzhorni* show a strong preference for tree holes and males for open foliage sites in Mandena, whereas there appears no sex-specific differentiation in *M. tanosi* (Lahann, 2008). Likewise, *Pandanus* plants are utilised to a much lesser extent by *M. ganzhorni* than by *M. tanosi*, who habitually use them in Sainte Luce, making up over 50% of all observed sleeping sites. *Microcebus tanosi* also appear to exhibit a less gregarious character. Such innate behavioural discrepancies may explain the disparate population densities of both species (Ganzhorn et al, 2008), with *M. ganzhorni* perhaps exhibiting a broader inherent metabolic and thermoregulatory capacity (Schmid, 2000; Lahann, 2008). This is consistent with the idea that *M. tanosi* are largely a rainforest specialist species, better adapted to large and consistently productive forests inland rather than the relatively unproductive coastal littoral forests (Bollen and Donati, 2005). Indeed, the dynamic history of the southern littoral forests over the past few thousand years, marked by periods of reduced precipitation and drought, marine surges and human settlement (Virah-Sawmy et al, 2009), is thought to have led to the gradual break-up of contiguous littoral forest, severing its connection to the humid forests inland.

Today, the three main southern littoral forests (Sainte Luce, Mandena and Petriky) are each occupied by a distinct *Microcebus* species. It is hypothesised that the modern distribution of mouse lemurs in the region has been equally dynamic, with dry adapted species such as *M. murinus* migrating eastward, exploiting the gradually drying climate (Hapke et al, 2012) and potentially radiating into several novel forms (e.g. *M. ganzhorni* and *M. manitatra*). To better understand the ecological adaptability of *M. tanosi* and its capacity to persist in restricted littoral habitats, additional studies at other sites (e.g. the humid rainforests of the Vohimena mountains) may yield interesting comparative data. Similarly, the distributional overlap and boundaries between *M. tanosi* and *M. rufus*, a closer genetic relative than *M. ganzhorni* (Yoder et al, 2016), in the northern parts of its rainforest range are presently unclear. To what extent these species demonstrate homogenous social and ecologically adapted behaviours provides an interesting avenue for future enquiry.

Microcebus tanosi utilise a wide array of tree and plant species as sleeping sites in Sainte Luce, similar to other *Microcebus* species elsewhere (e.g. Radespiel, 2000; Génin, 2010, Karanewsky and Wright, 2015; Hending et al, 2017), but demonstrate a clear preference for foliage type sites over tree holes. Although this study only provides a seasonal snapshot of the species' behaviour, and it is plausible that sleeping habits and behavioural strategies vary over the year (Pages-Feuillade, 1988; Radespiel, 2000; Lahann, 2008), as both thermoregulatory demands and reproductive phases change, it is evident that sleeping sites are predominantly selected for their anti-predatory characteristics during the austral summer. Similarly, a number of other key behavioural traits which may be viewed as adapted evolutionary strategies, related to sleeping ecology, support a scenario whereby predator avoidance is the primary selection criterion. Besides from preferentially opting for foliage type sites, which provide less thermal stability than tree holes (Schmid, 1998) but a better vantage point, focal individuals were observed to frequently change sleeping site, demonstrated high levels of sleep site sharing and selected sleeping sites with defensive attributes, within dense patches of forest. Combined, these behaviours lower the susceptibility of individuals to predation by limiting detection and access, through increased crypsis, hiding and escape capacity (Vine, 1973; Cowlinshaw, 1994), and dilute individual risk and increase vigilance through cohabiting (Hamilton, 1971; Janson, 1992). Within the relatively few species where sleeping behaviour has been studied so far, the majority (e.g. *M. berthae*, *M. lehilahytsara*, *M. rufus*, *M. sambiranensis*) appear to opt for foliage sleeping sites (Schwab, 2000; Jürges et al, 2013; Karanewsky and Wright, 2015; Hending et al, 2017), whilst *M. murinus* and *M. ganzhorni* (Radespiel et al, 2003b; Lahann, 2008) prefer tree holes. However, both *M. ravelobensis* and *M. griseorufus* appear to utilise both sleeping site types with relatively frequency

(Radespiel et al, 2003b; Génin, 2010). Although it is tempting to view these trends based on phylogenetic relationships (Kappeler, 1997; Bearder, 1999), further studies are required to comprehensively cement this pattern.

This study also found evidence for sex-specificity in terms of sleeping site selection by *M. tanosi*, with female individuals selecting sites with a combination of microhabitat characteristics that are significantly different from male individuals. Females selected sites with a suite of traits relating to tree size (greater tree height, broader crown widths and larger diameters). This is perhaps best explained in terms of differentiated reproductive strategies between the sexes, with males more likely to increase risk taking in search of receptive females and settling for lower quality sleeping sites as they roam larger and perhaps less familiar home ranges. Similarly, with females also relying on sleeping sites to raise and cache young, secure and better protected sleeping sites are a crucial Darwinian consideration (Radespiel et al, 1998; 2003b; Kappeler, 1998; Schmid, 1998). As well as providing better protection from predators (improved concealment), larger trees may also provide increased space and opportunity for cohabitation and therefore thermoregulatory behaviour, and feeding, with larger trees yielding more fruits and potentially harbouring greater invertebrate abundance. Such sex-specific habitat selection has also been observed in *M. murinus* in Ankarafantsika NP (Radespiel et al, 1998), but was not detected in a study of *M. sambiranensis* in Anabohazo (Hending et al, 2017). Whilst this study did not find any difference in the specific sleeping site type used between the sexes, it clearly highlighted the importance of a particular plant species, *Pandanus dauphinensis*. A highly abundant plant in the southern littoral forests, armed with a suite of defensive traits, this screwpine appears to act as a surrogate for tree holes, with the possible advantage of superior defensive attributes at the expense of thermoregulatory capacity. Examination of the literature suggests that other mouse lemur species also utilise Pandanaceae species (Lahann, 2008; Jürges et al, 2013; Karanewsky and Wright, 2015) and that the genus may play an important ecological and even evolutionary roles for mouse lemurs.

Predation is evidently an important factor governing species behaviour (van Schaik, 1983; van Schaik and van Hooff, 1983; Isbell, 1994; Wright, 1998), and it is clear from the results of this study that *M. tanosi* experiences high predation pressure in Sainte Luce, as elsewhere (Goodman et al, 1993; Karpanty and Wright, 2007). Indeed, the littoral forests support a large assemblage of candidate predator species (see **Chapter 2**, **Predators**), providing a threat during all activity phases. Whilst mortality is likely modulated to some extent by the predator community present, many important mouse lemur predators are common across Madagascar's forests (e.g. *Asio madagascariensis*, *Otus rutilus*, *Polyboroides radiatus*, *Ithycyphus* sp., *Sanzinia* sp.). At present,

the mortality rate of *M. tanosi* in Sainte Luce is unknown and very difficult to assess with any degree of certainty. However, it is clear that *M. tanosi*, like other mouse lemur species, constitutes an important trophic link in the littoral forest ecosystem, functioning as both a prey species and predator in its own right.

Curiously, the small number of leaf nests observed in this study were not located in specifically dense areas of forest, and often appeared to be relatively visible. Further study of the microhabitat characteristics surrounding leaf nests is required in order to determine what habitat variables are important in relation to these structures. Whilst the structure and form of the nests appears to be similar to those described as being used by other *Microcebus* spp. in terms of size and materials (Martin, 1972b; Atsalis, 1998; Weidt et al, 2004), the construction process was never directly observed. The limited number of nests documented in this study precluded thorough analysis but also raised questions relating to their specific function. Are they purely an alternative sleeping habitat with enhanced thermoregulatory and social benefits (Arnold, 1990; Blumstein et al, 2004), or are they constructed for specific purposes, and if so, how do they relate to other social and Darwinian behaviours? During this study a variety of individual sleeping configurations were observed utilising nest structures, indicating a non-reproductive function. Similarly, no neonate observations were made, suggesting that nests may not serve as nurseries. Furthermore, the architects of the nests remain unknown, and discovering how nest construction relates to sex could have significant implications for understanding the reproductive strategy of the species. It is also unclear whether individuals are responsible for constructing single or multiple nests, and how this behaviour corresponds to an individual's ranging behaviour. Whilst these questions may only be answered through chance observation, or in captive studies, further behavioural insight may be captured post construction by means of remote infra-red camera study. Such a study could shed light on the private lives of this highly secretive species, and further advance our knowledge of the social strategies of this highly cryptic and ancestral primate genera.

Beyond the scheduling limitations associated with the telemetric elements of this study, where data collection was largely restricted to the austral summer and where the necessity of thermoregulatory stability is perhaps ameliorated, a variety of other challenges may have affected the results. Battery constraints, governed by the weight limitations of the radio-collars, difficulties associated with capture and recapturing animals and general field conditions (e.g. storms and prolonged periods of rain) over the two year study period, meant that a selection of different focal individuals were observed instead of a consistent study cohort. Similarly, a small number of focal animals disappeared during the study and it is unclear whether they were predated and removed

from the local area or were lost as a result of malfunctioning radio-collars. These factors limited the capacity of the study to understand social interactions. Furthermore, the learning curve associated with collaring mouse lemurs meant that some individual animals escaped their collars in the initial months, setting the project back in time as further trapping became necessary. Locating focal animals at their sleeping site was also a significant challenge. As a result, it was difficult to ascertain with confidence whether an animal was either concealed within a tree hole high up in a tree, or merely concealed high in the foliage and out of sight of the observer. The lack of visual confirmation at a large number of sleeping sites limited the power of subsequent analysis.

Whilst this study has focused on several important aspects of mouse lemur social behaviour, other key ecological aspects of mouse lemur ecology proved difficult to address. Near to the top of this list is diet. Theoretically, small bodied primates are expected to focus on nutritionally dense food items such as arthropods to fuel their high metabolic requirements (Hladik, 1979; Clutton-Brock and Harvey, 1983; Kay, 1984). However, fruit is known to form a substantial proportion of the diet in other studied mouse lemurs (Martin, 1972b; Hladik et al, 1980; Atsalis, 1998). Whilst the degree of invertebrate consumption provides an important study topic on its own, reliable conclusions were prevented in this study by a paucity of observational data. Despite a considerable amount of time and effort invested in the tracking and observation of focal individuals throughout the study, direct feeding observations were seldom witnessed and only a limited inventory of feeding items was generated (see **Appendix**; **Table 1**). Visibility in the dense forest was a significant obstacle to obtaining a comprehensive image of the dietary habits of the species, and similarly, the difficulties associated with live trapping meant that fecal samples were not readily available for study (Atsalis, 2008). The results compiled by means of opportunistic observation however confirm the omnivorous or fauni-frugivorous nature of *M. tanosi*, setting it in line with other well studied mouse lemur species (Corbin and Schmid, 1995; Atsalis, 1998; Reimann et al, 2003; Radespiel et al, 2006; Dammhahn and Kappeler, 2008; Lahann, 2008). Whilst arthropod predation was occasionally observed (Araneae spp., Blattodea spp., Coleoptera spp., Hemiptera spp., Lepidoptera spp., Orthoptera spp.), consumption of both ripe and unripe fruits, flowers, buds and nectar were more common. Of the 16 food plant species observed in Sainte Luce, a small number appear to be consumed frequently, and include a number of common species that are abundant near the forest edge: *Vaccinium laevigatum*, *Sarcolaena multiflora*, *Leptolaena delphinensis*, *Saldinia littoralis* and *Aphloia theaeformis*. In Nahampoana, several mouse lemurs were observed with the yellow pollen of *Brexia madagascariensis* covering their

faces, suggesting they likely fulfil important ecological roles, as both pollinators and seed dispersers (Ramananjato et al, 2020).

Since this study was conducted largely during the austral summer, it is perhaps not surprising that most dietary observations were botanical. During this period, the southern littoral forests are most productive (Bollen and Donati, 2005). However, in order to better understand the species true diet, future studies should encompass the cooler winter period, when alternative food sources may be more important. Although some insight into a species dietary habits may be gained from study of its dental morphology (Martin, 1995), a more detailed assessment may be gained through non-invasive methods (Whitaker, 1988; Nekaris and Rasmussen, 2001; Atsalis, 2008). Since invertebrate feeding events are rarely observed (Kunz and Whitaker, 1983; Williamson et al, 1990), long-term studies based on fecal analysis may be the most effective way to accurately expose a species' diet, especially if genetic tools can be employed (Rowe et al, 2021). However, collecting sufficient samples still provides a substantial challenge. Incidentally, there were no observations of mouse lemur predation on small-bodied vertebrate prey during this study, as reported elsewhere (e.g. on *Gekkonidae* spp. and *Suncus* spp. SHR pers. obs.). Indeed, vertebrate predation may be more prevalent in the dry western forests of Madagascar, or during the austral winter when resource availability is limited (Bollen and Donati, 2005). Similarly, no gum (a high energy food source comprising of complex polymerized sugar exudates) feeding observations were recorded.

In this study, the population dynamics of three nocturnal lemur species, including *M. tanosi*, were modelled and used as a proxy for measuring the immediate impact of the protective status on a range of littoral forest fragments and to inform conservation management. Whilst these species offer only a partial view into the wider ecological dynamics of the littoral environment, they serve as a useful model as they represent species towards the higher end of the trophic spectrum, play important ecological roles (Fietz and Ganzhorn, 1999; Atsalis, 2008; Norscia et al, 2012; Ramananjato et al, 2020), and exist at densities whereby a change in population level signal may be detectable. No significant differences were observed within the nocturnal lemur communities between the four years prior to and after formal protection measures were introduced. Importantly however, results demonstrate that the sub-populations of each species are dynamic, fluctuate frequently and are independent of one another and of forest fragment. Whilst the population trends of *Microcebus tanosi* are difficult to interpret due to the limited number of observations, sub-population estimates appear largely consistent over the study and across the three study forest fragments. Conversely, whilst *Cheirogaleus thomasi* numbers in the larger protected fragment S9

appear stable, populations in both the heavily disturbed community resource forest S7 and the smaller protected fragment S8 appear to be burgeoning. Notably, a plantation of *Grevillea robusta* situated immediately adjacent to the forest edge in S8 appears to have opened up a new food resource that the dwarf lemurs are exploiting as they emerge from hibernation (S. Hyde Roberts. pers. obs). In light of these observations, such plantations could form part of a broader conservation strategy for these Endangered lemurs. In contrast, the projected outlook for the population of *Avahi meridionalis* in Sainte Luce is more perilous. The sub-population is S7 appears to be on the brink of extirpation, with only a handful of observations made over the past decade, whilst the sub-population in the largest protected fragment S9 also appears to have declined substantially over the study period. The cause of the decline is unclear, particularly as the smaller sub-population present in S8 appears to have remained relatively stable.

Results indicate that each species is responding to a different set of specific ecological factors, unique to each fragment, rather than a single universal or overarching driver. This could be anticipated to some extent given that species express distinct life history traits and are subject to differentiated ecological pressures. Furthermore, fragmented forests tend to vary in terms of biodiversity, anthropogenic influence and constituent environmental features. As a result, local factors have a differentiated effect on a species population turnover (Altmann and Altmann, 1979; Lee and Kappeler, 2003; Strier, 2003; Erhart and Overdorff, 2008; Wright et al, 2012). Although long-term monitoring studies on lemurs are relatively rare, these findings appear consistent with other projects, with the principal commonality that populations experience pronounced temporal fluctuation in population density (Ganzhorn et al, 2008; Erhart and Overdorff, 2008; Wright et al, 2012). Whilst other studies have largely focused on diurnal and cathemeral group living species (Erhart and Overdorff, 2008; Wright et al, 2012; Donati et al, 2017; 2020), this study focuses solely on the nocturnal lemur community and the inter-species dynamics and effects of habitat fragmentation and protection policy. Whilst the factors contributing to population turnover may fundamentally be related to diet (Eppley et al, 2020), climatic cycles (Wright et al, 2012) and the social and habitat requirements of each species (Lahann, 2008), the protected status and management regime of each forest fragment further modulates ecological interactions (i.e. determines habitat condition, disturbance level and may affect community diversity). Therefore, a fully enforced protective status does not necessarily guarantee a positive conservation outcome in terms of increased lemur population size and density, and vice versa. Whilst there are a number of methodological caveats necessary when interpreting the data, the results emphasise the long-term nature of human policy intervention and further underline the challenges associated with disentangling the downstream consequences from natural stochastic signals.

The low, but consistent number of mouse lemur observations recorded across this study reflects either a highly restricted and threatened population or is indicative of an inappropriate methodology. Whilst anecdotally, the mouse lemur population in Sainte Luce is greater than the modelled population estimates suggest (with frequent observations near forest edges and at shared sleeping sites) and alternative methodologies are necessary to corroborate these findings. Whilst Distance sampling appears to work well for mouse lemur species elsewhere in Madagascar (Nash, 2000; Radespiel and Raveloson, 2001; Ganzhorn et al, 2008; Malone et al, 2013), and for the other two larger bodied, nocturnal lemur species in Sainte Luce (*A. meridionalis* and *C. thomasi*), a few other studies have suggested methodological limitations relating to the genus (Müller et al, 2000; Radespiel et al, 2001b). The addition of habitat edge orientated transects may yield an increase in mouse lemur observations. Alternatively, the use of thermal imaging equipment and camera traps could provide cross-validation (Silveira et al, 2003; Olson et al, 2012; Gerber et al, 2014; Howe et al, 2017; Jumail et al, 2020). In the case of *M. tanosi* in the littoral forests of Sainte Luce, given the longitudinal nature of the study, the consistent low encounter rates observed in this study and those previous (Ganzhorn et al, 2008), it can be parsimoniously concluded that the population density is genuinely very low. This study concludes then that *M. tanosi* requires careful monitoring and should be regarded as a priority species for local conservation efforts.

The arrival of Rio Tinto (QMM) in the southeast of Madagascar set into motion a series of long-term environmental decisions with long lasting ecological effects that are set to play out for decades if not centuries to come. Whilst the mining programme has committed to achieve a net positive impact on biodiversity and recognise the negative impacts of landscape scale habitat alteration (Lowry and Faber-Langendoen, 1991, Lewis Environmental Consultants, 1992; QMM, 2001; Temple et al, 2012), the long-term survival of many species and the resulting ecological implications remain unclear. The loss of biodiversity and forest habitats as collateral appears to be an acceptable political trade-off for the economic stimulus the mine will bring to the local economy and communities. However, with a rapidly growing human community dependent on natural forest resources (Vincelette et al, 2007), the sustainability and ethics surrounding the mine remain contested (Virah-Sawmy, 2009b; Watson et al, 2010). In the specific context of Sainte Luce, preparations for the mining operation have precipitated the endorsement of protected status being applied to a number of forest fragments. Whilst these relict and isolated forests may provide a temporary ark for many species, encapsulating an ecosystem in microcosm, their long-term survival is unclear (Ganzhorn and Goodman, 2000; Lehtinen et al, 2003; Watson et al, 2005; Lehman et al, 2006).

The formation of protected areas is an undoubtedly important tool in conservation strategy (Chape et al, 2005), safeguarding the full set of species interactions and ecological relationships within designated borders. However, the parameters that define a protected area (e.g. size, condition, habitat connectivity and level of human interaction) are fundamental to the long-term success of the intervention, as is its subsequent management (Rodrigues et al, 2004; Cantu-Salazar and Gaston, 2010; Anthony and Szabo, 2011). Although the proposed protection of five forest fragments in Sainte Luce dates back to the early 2000's, only as of 2015 were formal measures introduced on the ground. As a result, logging activity and the harvesting of natural forests resources has largely ceased in the conservation zones, however local demand has not waned, and pressure has merely shifted to community forests. Given that the community forests sit within the proposed mining footprint, the strategy of preserving intact examples of littoral forest as conservation zones broadly appears to be working in the short term. However, understanding the effectiveness of conservation interventions, especially those involving threatened and biodiverse habitats and that impact upon sensitive and reliant communities, is a crucial measure of the success of long-term environmental strategy. Whilst QMM, the managers of the protected areas, have outlined a path towards achieving a net positive impact on biodiversity (QMM, 2001; Temple et al, 2012), the long-term solution to providing local communities with sustainable resources remains unclear, yet forms a fundamental part of the conservation puzzle. Furthermore, the modern assessment of biodiversity in Sainte Luce outlined in this study (**Chapter 7**) indicates a surprisingly precipitous decline in recent decades.

This study concludes that under the present scenario, whereby unsustainable community resource use remains unaddressed, and the mine's proposed activity is realised, a large number of species are at risk (Ganzhorn and Goodman, 2000; Ganzhorn et al, 2001; Bollen and Donati, 2006; Consiglio et al, 2006). Many species appear to have already disappeared from the area in recent decades, including Critically Endangered species (e.g. *Anas melleri*), several ecologically important taxa (e.g. *Accipiter henstii*, *Cryptoprocta ferox*) and potentially species that may have provided future ecotourism and economic appeal (e.g. *Cheirogaleus major* and *Hapalemur meridionalis* have both been appeared on inventories for Sainte Luce, however doubt surrounds these early identifications). Whilst the initial commitment to preserving biodiversity (Temple et al, 2012) is an important acknowledgement of the mines impact, several crucial decisions relating to wildlife remain unclear. As mining operations proceed, and a number of forest fragments are cleared, what will become of the myriad threatened animals that these forests support? Notwithstanding an unlikely capture and release project, it seems inevitable that many species will be pushed closer to extirpation. Given the limited extent of forest habitat anticipated post-

mining, and the large number of threatened species, even the prospect of intervention is not without risk. The mass translocation of species could expose communities to unpredictable ecological cascade effects (Terborgh et al, 2001; Estes et al, 2011; Colman et al, 2014). However, the transfer of large numbers of animals from one forest fragment to another seems one of only a few limited options. Translocations are evidently viewed as an important mediation tool, and thorough long-term monitoring of *Eulemur collaris* in Mandena has shown it can be successful, albeit not without some difficulties (Donati et al, 2007; 2020). Yet, it must be acknowledged that monitoring multiple species, many of which are smaller, more cryptic and are ecologically poorly understood, ultimately may not be feasible.

In parallel to direct conservation actions, the hard problem of addressing local community resource demands must also be met. With a substantial proportion of local communities living below the poverty line and reliant on forest resources (Vincellete et al, 2007c), failure to develop a sustainable alternative to diminishing forest materials will undermine any conservation efforts. Post mining, with only a handful of protected forest fragments remaining (Temple et al, 2012), the source of vital community resources is unclear. As a result, an ambitious and largescale reforestation project, encompassing all stakeholders and led by the local community, is a key priority for the area. Ultimately, severing the connection between the forest and the local communities who depend upon them is idealistic and unsustainable, and so a reliance on Protected Areas and 'fortress' style conservation, where large expanses of habitat are protected by restricting human activities, cannot be the long-term solution for Sainte Luce. In addition to the proposed forest restoration projects of QMM (Temple et al, 2012), establishing a mixed species plantation forest (using both native and endemic species), large enough to sustain moderate community usage and positioned strategically to encourage community use and at the same time maximise some species dispersal, is crucial. Furthermore, mechanisms whereby community wood collectors are obliged to contribute to forest maintenance (e.g. planting seeds) as part of their contract to harvest resources should be considered by the community natural resource committee (Communauté de Base or COBA). Faced with such a variety of challenges, biodiversity conservation in the littoral forests is deeply complex. The development of future conservation strategies in Sainte Luce clearly mandates very careful consideration, must embody the consensus view of major stakeholders, and address both biodiversity and community resource and development issues simultaneously. The coming decade represents an important juncture for the future of Sainte Luce, both in terms of the human community and its rich biodiversity, and decisions that are made now are likely to significantly shape the long-term future of the area.

In the context of lemur conservation, all four species presently occupying the area will require some form of intervention and management over the coming decades. With dispersal limited between the isolated forest fragments, population viability is a serious threat to long-term survival (Ganzhorn and Goodman, 2000). Significant reforestation efforts are required in conjunction with a strategy of maximising forest connectivity. The population data presented in this study provides an initial framework on which to base future conservation actions. Widely heralded as flagship species, lemurs often represent entire ecosystems and are used to attract the attention of ecotourists and funding bodies alike. As such, conservation initiatives involving lemurs are a useful means of protecting wider ecological communities (Durbin, 1999; Jolly et al, 2006; Zimmermann and Radespiel, 2014). Furthermore, their ecological roles are vital to the maintenance and function of the forest (Bollen et al, 2004; Bollen and Donati, 2006; Ramananjato, 2020). At present, all protected forest fragments in Sainte Luce support a full assemblage of lemur species, after an unexpected natural dispersal event of *Eulemur collaris* between S9 and S8 (Hyde Roberts et al, 2020), although the long-term fate of the migrant *Eulemur* group in S8 remains uncertain.

Whilst broad initiatives that benefit a wide range of taxa are ultimately preferable, smaller-scale species-specific projects are also vital. For example, the prospect of reintroducing the two extirpated lemur species (*Cheirogaleus major* and *Hapalemur meridionalis*) into Sainte Luce presents a realistic future opportunity, not only to recover and expand the distribution of the Endangered species, but also to restore ecosystem completeness and provide greater ecotourism appeal. However, a full review of the potential ecological effects of such a major intervention, both on existing communities and the imported species would be a necessity beforehand, as well as developing a robust understanding of the original extirpation causes. It must be noted that many Malagasy communities now rely heavily on the ecotourism sector, and this is set to increase in the future as more communities and protected areas tailor their economies towards securing income generated in this way. However, the sector is vulnerable to both national and international market instability, as experienced during the national coup d' état in 2009 (Schwitzer et al, 2014) and the coronavirus pandemic of 2020 (Buckley, 2020; Cherkaoui et al, 2020; Fletcher et al, 2020). Any proposed translocation program must recognise long-term responsibility and would require significant research into the suitability and sustainability of the donor habitat and the subsequent ecological impacts (Donati et al, 2007; 2017; 2020; Day et al, 2009; Schwitzer et al, 2013). Whilst such projects are ultimately attractive, a clearer picture of the littoral forest landscape in Sainte Luce post mining is necessary, with reintroduction into a stable network of protected, connected and regenerating forests providing a more agreeable proposal. In the

protected fragment S8, work is already underway to establish a series of small-scale habitat corridors. This work, undertaken by SEED Madagascar, primarily aims to facilitate the dispersal of nocturnal lemurs isolated within small forest patches, connecting four forest remnants to the main body of S8. The project further aims to encourage wider reforestation within the protected area and to develop a methodology for effectively bridging across areas of barren matrix habitat.

Devising specific conservation strategies for *Microcebus tanosi* in the littoral forests is not straightforward but appears to be of great importance. Despite the seemingly limited population, *M. tanosi* appears to occupy all surveyed forest fragments in Sainte Luce. The species appears to persist even within vestiges of forest, at least temporarily and like other *Microcebus* species seems able to utilise even the simplest habitat connections (Knoop et al, 2018; Schüßler et al, 2018). However, the progress of the mine dredge presents a huge threat to a large number of individual mouse lemurs. The large distance between many of the forest fragments, barren and criss-crossed with water bodies, makes the task of driving animals between forests fragments problematic. Yet mining strategy must carefully consider a stepwise process that maximises the opportunity for natural animal movement into protected areas. However, this is unlikely to be feasible in many instances. Given the unknown ecological consequences of dramatically increasing the number of animals in any particular fragment, reforestation and forest expansion projects are now essential and should be prioritised initially around the protected areas, outside of the mining footprint. The prior collection of animals ahead of the mining operation will present a hugely arduous task, however it affords an opportunity to establish a captive study population. Although finding a willing and suitable institution or research facility may prove difficult and require substantial permission and funding, such an ex-situ community of lemurs would provide an important pool of study animals. Similarly, such a population would also provide security against future declines and local extirpations at a time in Madagascar's history when the natural environment is changing rapidly.

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APPENDIX

Table 1.

Recorded dietary items consumed by *Microcebus tanosi* in the littoral forests of Sainte Luce observed during the study. All floral records pertain to the consumption of buds, flowers and fruit. *A number of individuals at Nahampoana Private Reserve were covered in the pollen of this species. Count refers to the number of times the species / group was directly observed being consumed.

	Vernacular Name	Scientific Name	Food Item	Count
Floral species	Fandramana	*Aphloia theaeformis*	Buds / Fruit	4
	Fandrianakanga	*Polycardia phyllanthoides*	Flowers / Nectar	3
	Fantsikahitra	*Plectronia densiflora*	Flowers	1
	Fonto	*Leptolaena delphinensis*	Buds / Fruit	7
	Harongampanihy	*Psorospermum* sp.	Flowers	1
	Hazondroatry	*Noronhia* cf. *lanceolata*	Flowers / Nectar	1
	Kalavelo	*Suregada crenulata*	Flowers	1
	Mangavoa	*Saldinia littoralis*	Fruit	6
	Pimakarova	*Turraea lanceolata*	Flowers	3
	Ropasy	*Eugenia cloiselii*	Fruit	1
	Rotry	*Syzygium emirnense*	Buds	1
	Sarigiavy	*Malleastrum mandenense*	Flowers / Nectar	2
	Tsilanitria	*Vaccinium laevigatum*	Flowers / Fruit	14
	Vokarepoky	*Brexia madagascariensis*	Flowers	*
	Vondrozana	*Sarcolaena multiflora*	Buds / Flowers / Nectar	9
	Vopaky	*Uapaca ferruginea*	Flowers / Fruit	1
	Zahambe	*Phyllarthron ilicifolium*	Flowers / Nectar	2
	Order	Taxa		
Faunal species	Araneae	Spiders		2
	Orthoptera	Katydid's		2
	Blattodea	Termites + Cochroaches		4
	Lepidoptera	Hawk moths		2
	Hemiptera	Cichada		1

Table 2. Vernacular and scientific names for all tree species identified in the botanical assessment.

A complete list of validated tree species in the littoral forest fragments of Sainte Luce. Vernacular names matched with scientific names based on a collected herbarium and with the assistance of botanists from Kew Gardens (David Rabehevitra) and Missouri Botanical Gardens (MBG) (Richard Razakamalala). IUCN Redlist statuses downloaded on 04-04-2021.

Vernacular name	Scientific name	Family	Origin	IUCN Status
Akatamaimbo	*Croton moraharivensis*	Euphorbiaceae	Leandri, 1939	NA
Akondronala	*Ophiocolea delphinensis*	Bignoniaceae	H. Perrier, 1938	VU
Ambirimbarika	*Sideroxylon beguei* var. *saboureaui*	Sapotaceae	Aubrév, 1974	NA
Ambora	*Tambourissa purpurea*	Monimiaceae	(Tul.) A. DC, 1868	LC
Ampoly	*Vepris elliotii*	Rutaceae	(Radlk.) I. Verd, 1926	LC
Andriambolafotsy	*Croton louvelii*	Euphorbiaceae	Leandri, 1939	NA
Anjarezo / Handrarezo	*Erica* sp.	Ericaceae	NA	NA
Anjavidy	*Erica sparsa var. sparsa*	Ericaceae	Lodd, 1829	NA
Bagedakorova	*Psychotria* sp.	Rubiaceae	NA	NA
Bamby	*Anthostema madagascariensis*	Loganiaceae	Baill, 1858	NA
Bandro	*Diospyros* sp.	Ebenaceae	NA	NA
Belataka	*Crateva obovata*	Capparaceae	Vahl, 1794	LC
Belavenoka	*Noronhia* sp.	Oleaceae	NA	NA
Bemalemy	*Bembicia uniflora*	Flacourtiaceae	(H. Perrier) Capuron, 1940	LC
Berehoka	*Dombeya* sp.	Sterculiaceae	NA	LC
Beronono	*Trilepisium madagascariense*	Moraceae	DC, 1825	NA
Boakandambo	*Dypsis fibrosa*	Arecaceae	(C.H.Wright) Beentje & J.Dransfield, 1995	LC
Ditsaky	*Mammea sessiliflora*	Clusiaceae	(Poir.) Planch. & Triana, 1861	LC
Falinandro	*Dracaena reflexa* var. *angustifolia*	Conavallariaceae	Baker, 1875	LC
Falinandro sp.2	*Dracaena reflexa* var. *nervosa*	Conavallariaceae	H. Perrier	LC
Fandranabo	*Pandanus longistylus*	Pandanaceae	Martelli & Pic. Serm, 1951	EN
Fandrafa (Vakoa)	*Pandanus dauphinensis*	Pandanaceae	Martelli, 1951	LC
Fandrianakanga	*Polycardia phyllanthoides*	Celastraceae	(Lam.) DC, 1825	NT
Fangora	*Erythroxylum nitidulum*	Erythroxylaceae	Baker, 1883	NA
Fanola	*Asteropeia* sp.	Theaceae	NA	NA
Fanola fotsy	*Asteropeia multiflora*	Theaceae	Thouars, 1807	LC
Fanola mena	*Asteropeia micraster*	Theaceae	Hallier f, 1921	VU
Fantsikahitra	*Plectronia densiflora*	Rubiaceae	Baker, 1883	LC
Fatsikaidriaky	*Coptosperma* sp.	Rubiaceae	NA	NA
Fatsikaitra	*Gaertnera* sp.	Rubiaceae	NA	NA
Fantsikahitsyboaka / Fatsikaiboeka	*Peponidium* sp.	Rubiaceae	NA	NA
Fantsikaidroka	*Pseudopeponidium asosa*	Rubiaceae	Arènes, 1960	NA

Vernacular name	Scientific name	Family	Origin	IUCN Status
Fantsikohy	*Drypetes madagascariensis*	Euphorbiaceae	(Lam.) Humbert & Leandri, 1932	LC
Fantsiskandrongo	*Ophiocolea floribunda*	Bignoniaceae	(Bojer ex Lindl.) H.Perrier, 1938	LC
Farisaty	*Physena madagascariensis*	Capparaceae	Steud, 1857	LC
Fihamy	*Ficus polita*	Moraceae	Vahl, 1805	LC
Filao	*Casuarina equisetifolia*	Casuarinaceae	L, 1759	LC
Fitoravy	*Vitex chrysomallum*	Verbenaceae	Steud, 1841	LC
Fonofotonanahary	*Rhus taratana*	Anacardiaceae	(Baker) H. Perrier, 1946	LC
Fonto	*Leptolaena delphinensis*	Sarcolaenaceae	G.E.Schatz & Lowry, 2001	VU
Fonto sp.2	*Leptolaena pauciflora*	Sarcolaenaceae	Baker, 1883	LC
Fontonbavy	*Leptolaena* sp.	Sarcolaenaceae	NA	NA
Fontondahy	*Schizolaena elongata*	Sarcolaenaceae	Thouars, 1805	LC
Forofoka	*Diospyros myriophylla*	Ebenaceae	(H.Perrier) ined.	LC
Forofoka sp.2	*Diospyros* sp.	Ebenaceae	NA	NA
Fotsivavo	*Polyalthia madagascariensis*	Annonaceae	Cavaco & Keraudren, 1957	EN
Fotsyavalaky	*Croton* sp.	Euphorbiaceae	NA	NA
Hafopotsy	*Grewia delphinensis*	Tiliaceae	Capuron	VU
Harambilo	*Podocarpus madagascariensis* var. *procerus*	Podocarpaceae	Baker, 1891	NT
Haramboanja	*Cassine micrantha*	Celastraceae	Loes, 1893	NA
Harandrato	*Intsia bijuga*	Fabaceae	(Colebr.) Kuntze	NT
Harongampanihy	*Psorospermum* sp.	Clusiaceae	NA	NA
Haziny	*Symphonia* sp.	Clusiaceae	NA	NA
Hazigny Tomate	*Symphonia fasciculata*	Clusiaceae	(Noronha ex Thouars) Vesque, 1893	VU
Hazofotsy	*Ludia* sp.	Flacourtiaceae	NA	NA
Hazomainty	*Diospyros gracilipes*	Ebenaceae	Hiern, 1873	LC
Hazomainty sp.2	*Diospyros* sp.	Ebenaceae	NA	NA
Hazomalan	*Casearia nigrescens*	Flacourtiaceae	Tul, 1868	LC
Hazomamy	*Apodytes* sp. *nov*	Icacinaceae	NA	NA
Hazombaroa	*Foetidia obliqua*	Lecythidaceae	Blume, 1850	LC
Hazombato	*Campylospermum obtusifolium*	Ochnaceae	(DC.) Tiegh, 1902	NA
Hazondrano	*Mascarenhasia speciosa*	Apocynaceae	Scott-Elliot, 1891	LC
Hazondraotry	*Noronhia cf. lanceolata*	Oleaceae	H.Perrier, 1950	LC
Hazondroka	*Homalium nobile*	Salicaceae	Baill, 1886	VU
Hazongalala	*Tricalysia* cf. *cryptocalyx*	Rubiaceae	Baker, 1882	LC
Kabokala	*Cerbera venenifera*	Apocynaceae	(Poir.) Steud, 1840	NA

Vernacular name	Scientific name	Family	Origin	IUCN Status
Kaboky	*Voacanga thourasi*	Apocynaceae	Roem. & Schult, 1819	NA
Kalavelo	*Suregada crenulata*	Euphorbiaceae	Baill, 1861	NA
Kangy	*Rhus thouarsii*	Anacardiaceae	(Engl.) H. Perrier, 1944	LC
Katrafa	*Terminalia fatraea*	Combretaceae	(Poir.) DC, 1828	LC
Korofoky	*Diospyros subenervis*	Ebenaceae	(H. Perrier) G.E. Schatz & Lowry	VU
Lalona	*Weinmannia madagascariensis*	Cunoniaceae	DC, 1830	NA
Lamonty	*Flacourtia ramontchi*	Flacourtiaceae	L'Hér, 1786	NA
Lampivahatry	*Scolopia erythrocarpa*	Salicaceae	H. Perrier, 1940	EN
Lampivahatsymena	*Ludia antanosarum*	Salicaceae	Capuron & Sleumer, 1972	LC
Lendemibe	*Anthocleista madagascariensis*	Loganiaceae	Baker, 1882	LC
Lendemilahy	*Anthocleista longifolia*	Loganiaceae	(Lam.) Boiteau, 1973	VU
Lokaza	*Barringtonia asiatica*	Lecythidaeceae	(L.) Kurz, 1875	LC
Lona	*Oncostentum* sp.	Myrsinaceae	NA	NA
Mafotra	*Brochoneura madagascariensis*	Myristicaceae	(Lam.) Warb, 1897	NA
Magnarytoloho	*Dalbergia pseudomaritima*	Fabaceae	(R. Vig.)	NA
Malemiloha	*Alberta minor*	Rubiaceae	Baill, 1879	LC
Mampay	*Cynometra cloiselii*	Fabaceae	Drake	NA
Mampay rano	*Cynometra delphinensis*	Fabaceae	Du Puy & R.Rabev	NA
Manarano	*Beccariophoenix madagascariensis*	Arecaceae	Jum. & H.Perrier, 1915	VU
Mangavoa	*Saldinia littoralis*	Rubiaceae	Bremek, 1957	NA
Mantsa	*Memecyton* sp.	Delastomataceae	NA	NA
Memboloa	*Rinorea pauciflora*	Violaceae	(Thouars) Baill, 1886	NA
Menahihy	*Erythroxylon* sp.	Erythroxylaceae	NA	NA
Mokaranana	*Macaranga obovata*	Euphorbiaceae	Boivin ex Baill, 1861	LC
Nato	*Mimusops coriacea*	Sapotaceae	(A.DC.) Miq, 1863	NA
Nato' ala	*Faucherea* sp.	Sapotaceae	NA	NA
Nofotrakoho	*Vitex grandidiana*	Lamiaceae	W.Piep, 1929	EN
Nonoka	*Ficus reflexa*	Moraceae	Thunb, 1786	LC
Pandanus sp.3 (swamp - huge)	*Pandanus concretus*	Pandanaceae	Baker, 1885	LC
Pandanus sp.4 (branched)	*Pandanus* sp.	Pandanaceae	NA	NA
Pandanus sp.5 (triangle)	*Pandanus* sp.	Pandanaceae	NA	NA
Pimakarova	*Turraea lanceolata*	Meliaceae	Cav, 1789	VU
Ramirisa	*Homalium louvelianum*	Flacourtiaceae	H. Perrier, 1940	VU
Ramy	*Canarium boivinii*	Burseraceae	Engl, 1883	NA

Vernacular name	Scientific name	Family	Origin	IUCN Status
Raobe	*Dypsis nodifera*	Arecaceae	Mart, 1849	LC
Raotry	*Dypsis scottiana*	Arecaceae	(Becc.) Beentje & J.Dransfield, 1995	VU
Ravenala	*Ravenala madagascariensis*	Strelitziaceae	Sonn, 1782	LC
Resonjo	*Beilschmiedia madagascariensis*	Lauraceae	(Danguy) Kosterm, 1952	LC
Resonjolahy	*Ocotea racemosa*	Lauraceae	(Danguy) Kosterm, 1939	LC
Robavy	*Syzygium bernieri*	Myrtaceae	(Baill. ex Drake) Labat & Schatz, 2002	LC
Ropasy	*Eugenia cloiselii*	Myrtaceae	H.Perrier, 1952	EN
Ropoaky	*Eugenia* sp.	Myrtaceae	NA	NA
Rotry	*Syzygium emirnense*	Myrtaceae	(Baker) Labat & Schatz, 2002	LC
Rotry rotry	*Syzygium* sp.	Myrtaceae	NA	NA
Sanira	*Tina thouarsiana*	Sapindaceae	(Cambess.) Capuron, 1969	LC
Sanirafotsy	*Astrotrichilia elliotii*	Meliaceae	(Harms) Cheek, 1989	EN
Saniramena	*Tinopsis conjugata*	Sapindaceae	(Thouars ex Radlk.) Capuron, 1969	LC
Saridobaka	*Lamiaceae* sp.	Lamiaceae	NA	NA
Sarigavo	*Malleastrum mandenense*	Meliaceae	J.-F.Leroy, 1964	VU
Sarihafts	*Peponidium densiflorum*	Rubiaceae	(Baker) A.P.Davis & Razafim	LC
Sarikaboky	*Tabernaemontana retusa*	Apocynaceae	(Lam.) Pichon, 1948	LC
Sarivotaky	*Tabanaemontana* sp.	Apocynaceae	NA	NA
Sarkafe	*Colea* sp.	Bignoniaceae	NA	NA
Sisikandrongo	*Poupartia chapelieri*	Lauraceae	(Guillaumin) H. Perrier, 1944	LC
Sitaky	*Scutia myrtina*	Rhamnaceae	(Burm. f.) Kurz, 1875	LC
Sivory	*Garcinia* sp.	Clusiaceae	NA	NA
Somotsoy	*Colea racemosa*	Bignoniaceae	(Lam.) Baill, 1887	NA
Sotro	*Phylloxylon xylophylloides*	Fabaceae	(Baker) "Du Puy, Labat & Schrire"	NT
Taholagna	*Hyperacanthus mandenensis*	Rubiaceae	Rakotonas. & A.P.Davis, 2004	VU
Tanatananala	*Psychotria lantzii*	Rubiaceae	Drake	LC
Tandrokosy	*Cabucala madagascariensis*	Rubiaceae	(A.DC.) Pichon, 1948	LC
Tapinandro	*Homalium albiflorum* var.*leucophleum*	Flacourtiaceae	(Tul.) H. Perrier, 1940	LC
Tapinandromadnedravy	*Homalium planiflorum*	Flacourtiaceae	(Boivin ex Tul.) Baill, 1886	LC
Tavolohazo	*Cryptocarya* sp.	Lauraceae	NA	NA
Telopoloambilany	*Dypsis saintelucei*	Arecaceae	Beentje, 1995	EN
Tsihanimposa	*Homalium involucratum*	Salicaceae	(DC.) O. Hoffm, 1881	LC
Tsikondriakondriky	*Colea obtusifolia*	Bignoniaceae	DC, 1845	NA
Tsilaka	*Morella spathulata*	Myricaceae	(Mirb.) Verdc. & Polhill, 1998	LC

Vernacular name	Scientific name	Family	Origin	IUCN Status
Tsilanitria	*Vaccinium laevigatum*	Ericaceae	Castigl, 1790	NA
Vahabatra	*Cinnamosma madagascariensis var.namoronensis*	Canellaceae	Danguy, 1910	LC
Vahimainty	*Flagellaria indica*	Flagellariaceae	L, 1753	NA
Vahimbokatepoka	*Dichapetalum madagascariensis*	Dichapetalaceae	Poir, 1819	NA
Vahy fotsy	*Jasminum kitchingii*	Oleaceae	Baker, 1881	NA
Vahy goneny	*Secamone* sp.	Asclepiadaceae	NA	NA
Vahy mara	*Baroniella camtocarpioides*	Apocynaceae	Costantin & Gallaud, 1907	NA
Vahy mena	*Plectaneia* sp.	Apocynaceae	NA	NA
Vahy sitaky	*Scutia maritima*	Rhamnaceae	Perkins, 1911	NA
Vakamainty	*Agelaea pentagyna*	Connaraceae	(Lam.) Baill, 1882	NA
Valipangaly	*Scolopia* sp.	Salicaceae	NA	NA
Valotsy	*Breonia* sp.	Rubiaceae	NA	NA
Varikanda	*Dillenia triquetra*	Dilleniaceae	(Rottb.) Gilg, 1893	LC
Varo	*Hibiscus tiliaceus*	Malvaceae	L, 1753	LC
Varongy	*Ocotea* sp.	Lauraceae	NA	NA
Voakarepoky	*Brexia madagascariensis*	Celastraceae	(Lam.) Thouars ex Ker Gawl, 1823	LC
Voankazonala	*Homalium moniliforme*	Flacourtiaceae	H. Perrier	LC
Voapaky	*Uapaca ferruginea*	Euphorbiaceae	Baill, 1858	LC
Voapaky sp.2	*Uapaca littoralis*	Euphorbiaceae	Denis, 1927	LC
Voatsilana	*Polyscias aculeata*	Araliaceae	(Decne. & Planch.) Harms, 1894	LC
Voatsilana sp.2 (lahy)	*Schefflera rainaliana*	Araliaceae	Bernardi, 1980	EN
Vondrozana	*Sarcolaena multiflora*	Sarcolaenaceae	Thouars, 1805	LC
Voroatsy	*Syzygium* sp.	Myrtaceae	NA	NA
Voromy	*Antidesma madagascariensis*	Euphorbiaceae	Lam, 1783	NA
Vosiho	*Bruguiera gymnorhiza*	Rhizophoraceae	(L.) Lam, 1798	LC
Votaky	*Strychnos spinosa*	Loganiaceae	(L.) Lam, 1794	NA
Za	*Dialium madagascariensis*	Fabaceae	Baill	NA
Zaha	*Phyllarthron madagascariensis*	Bignoniaceae	K. Schum, 1895	NA
Zahambe	*Phyllarthron ilicifolium*	Bignoniaceae	(Pers.) H.Perrier, 1936	EN
Zahambe Siriky	*Phyllarthron* sp.	Bignoniaceae	NA	NA
Zambo	*Grisollea* sp.	Icacinaceae	NA	NA
Zora	*Homalium planiflorum*	Flacourtiaceae	(Boivin ex Tul.) Baill, 1886	LC
Zorafotsy	*Noronhia ovalifolia*	Oleaceae	H.Perrier, 1950	EN
Zoralahy	*Dicoryphe stipulacea*	Oleaceae	J.St.-Hil, 1805	LC
Zoramena	*Scolopia orientalis*	Flacourtiaceae	Sleumer, 1972	VU

Copies of Research Permits and invitations used throughout the study.

REPOBLIKAN'NY MADAGASIKARA
Fitiavana-Tanindrazana- Fandrosoana

SECRETARIAT GENERAL

DIRECTION GENERAL DES FORETS

DIRECTION DU SYSTEME DES AIRES PROTEGEES

AUTORISATION DE RECHERCHE

N°260/18/MEEF/SG/DGF/DSAP/SCB.Re
(Renouvellement de l'AR N°142/17 du 06/06/2017)

NOM	ROBERTS
PRENOM	Sam Hyde
ADRESSE	Université Antananarivo B P 906
FONCTION	Chercheur
ACCOMPAGNE DE	Giuseppe Donati, un étudiant de MZBA
ORGANISME TUTEL	Mention: Zoologique et Biodiversite Animale (MZBA)
LIEU	Forêt de Sainte Luce
DUREE	Six (06) mois à partir d'Octobre 2018

EST AUTORISE (E) A FAIRE DES RECHERCHES SUR:
« Une enquête sur la flexibilité écologique du Microcebus sp .trouvé à St Luce, au Sud-est de Madagascar ; premières recherches sur l'utilisation de l'habitat, le territoire et l'alimentation de l'écologie dans un paysage fragmenté »

MENTION SPECIALE D'ACTIVITES
Détermination des caractères écologiques du *Microcebus sp*, de la densité ainsi que la taille de la population
Capture avec relâche d'au maximum douze (12) *Microcebus* dans deux fragments forestiers par piège Sherman après pose des radio-colliers (au maximum sur 6 individus), prélèvement d'échantillons de poils, tissus d'oreilles et fèces, suivi de l'animal focal et prise des données morphométriques, description des espèces
Etude génétique, phénologique des plantes, de l'alimentation et du mode de vie.
Etude de l'abondance des invertébrés par utilisation des pièges litière, pièges collants, et piège à lumière activé deux fois par mois
Etudier la variabilité biométrique du *Microcèbes*, élucider le niveau de compétition avec d'autres petits mammifères, enquête sur la sélection des sites de sommeil et écologie des nids
Localisés et détaillés les sites de nidification de tous les individus
Collecte de données sur la disponibilité alimentaire et la productivité forestière
Collecte d'échantillons botaniques liés à l'écologie alimentaire (feuilles, tiges, racines, fleurs) consommés par des microcèbes pour identification et analyses chimiques
AUCUN DEVELOPPEMENT DE PRODUITS N'EST AUTORISE

EXPORTATION : Un (01) échantillon de : (tissus d'oreilles, poils et de fèces) par individu de *Microcebus sp*, spécimens morts d'invertébrés consommées par le *Microcebus sp*, tissus végétaux consommées par l'animal (feuilles, tiges, fruits, fleurs et racines) (espèce à préciser par la DSAP après analyse du rapport préliminaire)

OBLIGATIONS DU TITULAIRE :
- Négocier avec les gestionnaires et/ou comité de gestion des sites ou forêts transférées pour y accéder, le cas échéant
- Faire viser la présente par la Direction Régionale de l'Environnement, de l'Ecologie
- et des Forêts et/ou CEEF concernées avant toute descente sur terrain conformément à la note **n° 394-10/MEF/SG/DGF/DVRN/SGFF du 18 Mai 2010** de la localité de recherche
- Remettre à la Direction du Système des Aires Protégées, en quatre (04) exemplaires EN FRANÇAIS, le rapport préliminaire à la fin de sa mission et le rapport final avec les résultats des recherches au plus tard UN ans après la mission, en versions papier et électronique.
- Respecter la réglementation en matière forestière
- Pour tout transport de produits de collecte (faune et flore), avoir un procès-verbal de constatation des collectes effectuées par le CEEF concerné et autorisation de transport délivré par DREEF si le déplacement se fait en dehors de la région et remettre une copie au DSAP
- Pour toute publication : référer le numéro et la date de l'autorisation de recherche
- Pour toute exportation : remettre une copie du dépôt au DSAP et une autre au dossier d'exportation

AMPLIATIONS :
CAFF/CORE
DREEF : Sud_Est
CEEF: concernées
Communes concernées
« Pour contrôle et suivi »
DGF
« Pour contrôle et suivi »
MZBA
« Pour le rapport»

Antananarivo, le 15 OCT 2018
LE DIRECTEUR DU SYSTEME DES AIRES PROTEGEES

RAKOTOARIDERA Rantonirina

Permit 1 of 3.

REPUBLIKAN'I MADAGASIKARA
Fitiavana-Tanindrazana–Fandrosoana

SECRETARIAT GENERAL

DIRECTION GENERALE DES FORETS

AUTORISATION DE RECHERCHE

DIRECTION DU SYSTEME DES AIRES PROTEGES

N° 142 /17/MEEF/SG/DGF/DSAP/SCB.Re

(Renouvellement de l'Aut N°195/16 du 29/08/2016)

NOM ROBERTS

PRENOMS Sam Hyde

ADRESSE B.P: 906 Antananarivo

FONCTION Chercheur

ACCOMPAGNE DE : Zafimahery Rakotomalala, Giuseppe Donati, un étudiant de MZBA, un représentant du CAFF/CORE.

ORGANISME TUTELLE : Mention: Zoologique et Biodiversite Animale (MZBA)

EST AUTORISE(E) A FAIRE DES RECHERCHES SUR:

Etude sur l'origine de la fragmentation des forêts littorales du sud-est de Madagascar : Utilisation de la diversification génétique du genre *Microcebus* en vue de reconstituer l'histoire de l'environnement des forêts littorales.

LIEU : Forêt de Sainte Luce.

MENTION SPECIALE EVENTUELLE:

Détermination des caractères écologiques du *Microcebus sp*, de la densité ainsi que la taille de la population
Capture avec relâche d'au maximum douze (12) *Microcebus* dans deux fragments forestiers par piège Sherman après pose des radio-colliers (au maximum sur 6 individus), prélèvement d'échantillons de : poils, tissus d'oreilles et féces
Suivi de l'animal focal et prise des données morphométriques, description des espèces,
Collecte d'échantillons de la nourriture consommée par l'animal pour analyses et identification des plantes et invertébrés
Etude de l'abondance des invertébrés par utilisation des pièges pitfall
Investigation sur : - la distribution spaciale et utilisation de l'habitat, la selection des sites pour dormir et écologie de l'allaitement
- les activités saisonières, des macros distributions de *Microcebes* à travers les forêts
- des populations de Sainte Luce.

Etude génétique, phénologique des plantes, de l'alimentation et du mode de vie.

EXPORTATION : Echantillons de : tissus d'oreilles, poils et de féces de *Microcebus sp*, spécimens morts d'invertébrés consommées par le *Microcebus sp*, tissus végétaux consommées par l'animal (feuilles, tiges, fruits, fleurs et racines).

DUREE : Six (06) mois à partir mois d'Août 2017.

OBLIGATION DU TITULAIRE :

- Négocier avec les gestionnaires et/ou comité de gestion des sites ou forêts transférées pour y accéder, le cas échéant
- faire viser la présente par la Direction Régionale de l'Environnement, de l'Ecologie, et des Forêts Anosy et/ou CEEF concernées avant toute descente sur terrain conformément à la note **n° 394-10/MEF/SG/DGF/DVRN/SGFF du 18 Mai 2010** de la localité de recherche
- pour tout transport de produits de collecte (faune et flore), avoir un **procès-verbal de constatation** des collectes effectuées par les CEEF et **autorisation de transport délivré par DREEF** si le déplacement se fait en dehors de la région et remettre une copie au DSAP
- Pour toute exportation : remettre une copie du dépôt au DSAP et une autre au dossier d'exportation
- Pour toutes publications, référer le numéro et la date de l'autorisation de recherche.
- remettre à la Direction du Système des Aires Protégées, en quatre (04) exemplaires EN FRANÇAIS, le rapport préliminaire à la fin de sa mission et le rapport final avec les résultats des recherches au plus tard UN ans après la mission, en versions papier et électronique.

Antananarivo, le 06 JUIN 2017

LE DIRECTEUR
DU SYSTEME DES AIRES PROTEGES

Le Directeur Régional de l'Environnement

ANDRIANTSALAMA RAMAKARARO Come

RAKOTOARIDERA Rantoniaina
Ingénieur des Eaux et Forêts

AMPLIATIONS :

- CAFF/CORE
- DREEF: Ans
- CEEF: concernées
- Commune concernées
  « Pour contrôle et suivi »
- DGF
- **« Pour contrôle et suivi »**
- MZBA
  « Pour le rapport »

Permit 2 of 3.

REPOBLIKAN'I MADAGASIKARA
Fitiavana-Tanindrazana–Fandrosoana

SECRETARIAT GENERAL

DIRECTION GENERALE DES FORETS

DIRECTION DU SYSTEME DES AIRES PROTEGEES

AUTORISATION DE RECHERCHE

N° 195 /16/MEEF/SG/DGF/DSAP/SCB.Re

NOM ROBERTS
PRENOMS Sam Hyde
ADRESSE B.P 906 Antananarivo
FONCTION Chercheur

ACCOMPAGNE DE : Zafimahery Rakotomalala, Guiseppe Donati,Etudiant de MZBA, un représentant du CAFF/CORE.

ORGANISME TUTELLE : Mention: Zoologie et Biodiversité Animale(MZBA)

EST AUTORISE(E) A FAIRE DES RECHERCHES SUR: Etude sur l'origine de la fragmentation des forêts littorales du sud-est de Madagascar: Utilisation de la diversification génétique du genre *Microcebus* en vue de reconstituer l'histoire de l'environnement des forêts littorales

LIEU : Forêt de Sainte Luce

MENTION SPECIALE EVENTUELLE:

Fournir des données qui aideront à résoudre les lacunes entourant la perte et la fragmentation des forêts littorales.
Comparaison des profils génétiques des espèces et des populations de *Microcebus* trouvées dans les forêts.
Utilisation du genre *Microcebus* comme outil pour afficher l'historique des différentes zones de la forêt.
Etude des limites de distribution de l'espèce dans les forêts de Sainte Luce.
Etude de l'hypothèse que plusieurs espèces de *Microcebus* ou même des hybrides sont sympatriques dans la région.Détermination de l'état de conservation, de la densité et de la dynamique des populations de l'espèce.
Enquête sur la séparation de l'espèce sur l'écologie alimentaire, la phénologie.
Etude de la communauté de rongeurs invasive de Sainte Luce (aspect accessoire du piégeage) en ce qui concerne la quantification de son impact écologique sur les zones d'espèces *Microcebus*.
Description des espèces et collecte de données morphologiques.
Capture avec des pièges Sherman appâtés sur 5 zones par jour.Chaque zone sera couverte, de manière simultanée par 20 pièges, soit 100 pièges au total.
Collecte d'échantillons de poils, tissus d'oreille et de fécès d'au maximum 05 individus par espèce de microcèbe dans chaque fragment de forêt.
Pose de petits radios colliers d'au maximum 05 individus de microcèbes capturé.

EXPORTATION : Echantillons de tissus d'oreille, de poils et de fécès de *Microcebus*

DUREE : Six (06) mois à partir du mois d'Aout 2016.

OBLIGATION DU TITULAIRE :

- Négocier avec les gestionnaires et/ou comité de gestion des sites ou forêts transférées pour y accéder, le cas échéant
- faire viser la présente par la Direction Régionale de l'Environnement, de l'Ecologie, et des Forêts ANOSY, et/ou CEEF concernées avant toute descente sur terrain conformément à la note **n° 394-10/MEF/SG/DGF/DVRN/SGFF du 18 Mai 2010** de la localité de recherche
- pour tout transport de produits de collecte (faune et flore), avoir un **procès-verbal de constatation** des collectes effectuées par les CEEF et **autorisation de transport délivré par DREEF** si le déplacement se fait en dehors de la région et remettre une copie à la DSAP
- Pour toute exportation : remettre une copie du dépôt à la DSAP et une autre au dossier d'exportation
- Pour toutes publications, référer le numéro et la date de l'autorisation de recherche.
- remettre à la Direction du Système des Aires Protégées, en quatre (04) exemplaires EN FRANÇAIS, le rapport préliminaire à la fin de sa mission et le rapport final avec les résultats des recherches au plus tard UN ans après la mission, en versions papier et électronique

Antananarivo, le 29 AOUT 2016

LE DIRECTEUR
DU SYSTEME DES AIRES PROTEGEES

RAKOTOARIDERA Antonirina
Ingénieur des Eaux et Forêts

AMPLIATIONS :

- CAFF/CORE
- DREEF: Ans
- CEEF: concernées
- QMM
- Communes concernées

« Pour contrôle et suivi »

- DGF

«Pour compte rendu»

Permit 3 of 3 - Research permissions granted by the Malagasy Ministry of Environment and Sustainable Development (Ministère de l'Environnement et du Développement Durable - MEDD) over the course of the study.

UNIVERSITE D'ANTANANARIVO
FACULTE DES SCIENCES
DOMAINE DES SCIENCES ET TECHNOLOGIES
MENTION ZOOLOGIE ET BIODIVERSITE ANIMALE
B.P. 906
101 ANTANANARIVO
(Madagascar)

Latimeria chalumnae

N° : 226 /ZBA/18/ZR

LETTRE D'INVITATION

Dans le cadre de l'Accord de Collaboration entre l'Université de OxfordBrookes, Angleterre, l'Université d'Antananarivo, l'Université d'Antananarivo qui est représentée par la Mention Zoologie et Biodiversité Animale de la Faculté des Sciences accepte la venue à Madagascar de l'étudiant chercheur de l'Université de OxfordBrookes, Monsieur **Sam Hyde Roberts**, et l'invite à effectuer des recherches pendant la période du :

01er Août 2018 au 01er Août 2019 à Sainte Luce.

Son thème de recherche est :

" Etude sur la flexibilité écologique du *Microcebus* sp. trouvé à Sainte Luce, sud-est de Madagascar; premières recherches sur l'utilisation de l'habitat, le territoire et l'alimentation de l'écologie dans un paysage fragmenté".

En foi de quoi, cette lettre d'invitation est délivrée pour lui servir et valoir ce que de droit.

Encadreur :

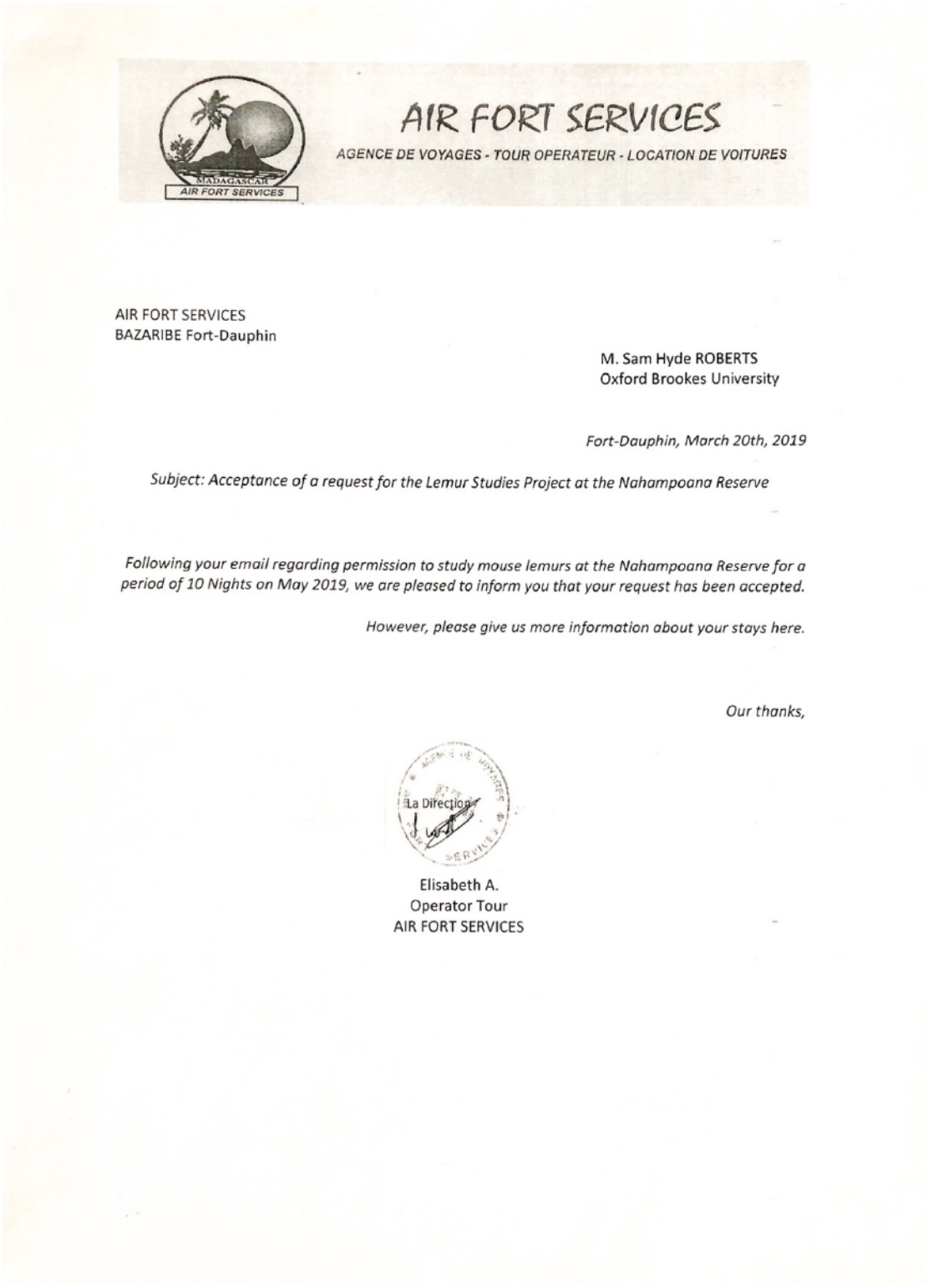
- Dr. Giuseppe Donati

Antananarivo le 16 Août 2018

Le Responsable de la Mention
"Zoologie Et Biodiversité Animale"

Dr. Rakotomalala Zafimahery

Letter 1 - Letter of invitation received from the University of Antananarivo to conduct research in lieu of a formal research permit between 01st August 2018 to 01st August 2019.



AIR FORT SERVICES

AGENCE DE VOYAGES - TOUR OPERATEUR - LOCATION DE VOITURES

AIR FORT SERVICES
BAZARIBE Fort-Dauphin

M. Sam Hyde ROBERTS
Oxford Brookes University

Fort-Dauphin, March 20th, 2019

Subject: Acceptance of a request for the Lemur Studies Project at the Nahampoana Reserve

Following your email regarding permission to study mouse lemurs at the Nahampoana Reserve for a period of 10 Nights on May 2019, we are pleased to inform you that your request has been accepted.

However, please give us more information about your stays here.

Our thanks,

La Direction

Elisabeth A.
Operator Tour
AIR FORT SERVICES

Letter 2 - Letter of invitation received from Air Fort Services, granting permission to expand my study to the privately managed reserve, Nahampoana

Table 3a.

Complete biometric analysis of the 42 *M. tanosi* individuals captured in the littoral forests of Sainte Luce between September 2015 and May 2019. Age classes based on description in Groves & Harding (2003) and assessment made in the field based on weight class. *Indicates combined adult and sub-adult individuals.

Locality	Sainte Luce (n=42)															
	Adult				Sub-adult				Juvenile				Infant			
	n	Min	Max	Mean ± SD	*n*	Min	Max	Mean ± SD	*n*	Min	Max	Mean ± SD	*n*	Min	Max	Mean ± SD
Body mass (sexes combined)	21	60.0	78.5	66.5 ± 4.8	14	41.0	59.0	50.5 ± 6.4	5	17.5	34.0	23.8 ± 6.8	2	13.5	14.1	13.8 ± 0.4
Body mass (female)	14	60.0	78.5	66.2 ± 5.4	10	41.0	59.0	50.0 ± 7.2	4	18.5	34.0	25.4 ± 6.7	-	NA	NA	NA
Body mass (male)	7	63.0	72.0	67.3 ± 3.5	4	47.0	56.6	51.7 ± 4.4	-	NA	NA	NA	-	NA	NA	NA
Body mass index (sexes combined)	21	3.059	5.230	3.884 ± 0.53	14	2.450	4.691	3.416 ± 0.74	5	2.225	3.416	2.738 ± 0.46	2	3.878	4.340	4.109 ± 0.33
Body mass index (female)	14	3.320	5.230	4.001 ± 0.48	10	2.594	4.691	3.412 ± 0.77	4	2.225	2.817	2.568 ± 0.33	-	NA	NA	NA
Body mass index (male)	7	3.059	4.823	3.642 ± 0.58	4	2.450	4.192	3.427 ± 0.79	-	NA	NA	NA	-	NA	NA	NA
Head and body length (sexes combined)	21	111.5	150.3	131.6 ± 10.0	14	111.0	138.5	122.6 ± 7.7	5	71.6	109.9	93.5 ± 16.4	2	57.0	59.0	58.0 ± 1.4
Head and body length (female)	14	111.5	140.0	129.1 ± 9.6	10	111.0	130.2	122 ± 6.9	4	81.9	109.9	99.0 ± 12.6	-	NA	NA	NA
Head and body length (male)	7	122.2	150.3	136.8 ± 9.2	4	113.5	138.5	124 ± 10.6	-	NA	NA	NA	-	NA	NA	NA
Tail length (sexes combined)	21	106.1	153.8	132.0 ± 11.6	14	116.0	150.6	128.8 ± 10.3	5	73.2	118.8	92.6 ± 18.4	2	57.0	65.0	62.0 ± 4.2
Tail length (female)	14	125.0	132.7	131.2 ± 10.0	10	116.0	150.6	126.0 ± 9.8	4	80.0	118.8	97.5 ± 17.2	-	NA	NA	NA
Tail length (male)	7	106.1	153.8	133.8 ± 15.0	4	123.0	143.5	135.8 ± 9.0	-	NA	NA	NA	-	NA	NA	NA
Tail width (sexes combined)	21	6.4	12.5	10.3 ± 1.8	14	5.7	10.8	8.5 ± 1.7	5	5.2	7.8	6.7 ± 1.0	2	4.0	4.0	4.0 ± 0.0
Tail width (females)	14	6.4	12.0	10.1 ± 1.6	10	5.7	10.8	8.2 ± 1.9	4	5.2	7.8	6.6 ± 1.1	-	NA	NA	NA
Tail width (males)	7	9.8	12.5	10.9 ± 2.2	4	8.5	10.0	9.3 ± 0.8	-	NA	NA	NA	-	NA	NA	NA
Total length (sexes combined)	21	235.2	298.5	263.7 ± 19.2	14	234.0	282.0	251.4 ± 15.4	5	144.8	228.6	186.1 ± 34.1	2	116.0	124.0	120.0 ± 5.7
Total length (female)	14	235.2	297.2	260.3 ± 17.3	10	234.0	281.2	248.0 ± 13.6	4	161.2	228.6	196.5 ± 29.0	-	NA	NA	NA
Total length (male)	7	236.5	298.5	270.6 ± 22.2	4	236.5	282.0	260.0 ± 18.6	-	NA	NA	NA	-	NA	NA	NA
Dorsal stripe length	21	80.2	97.3	87.1 ± 4.6	14	68.0	96.3	83.1 ± 8.4	5	72.0	79.3	74.8 ± 2.8	-	NA	NA	NA
Dorsal stripe width	18	4.3	8.6	6.4 ± 1.3	13	2.4	7.4	5.5 ± 1.8	4	3.9	4.9	4.9 ± 0.9	-	NA	NA	NA
Head length	14	31.4	44.0	37.8 ± 2.7	13	33.0	39.3	35.7 ± 2.2	4	32.2	37.0	34.6 ± 2.4	2	20.0	20.1	20.05 ± 0.1
Head width	14	21.3	30.0	24.8 ± 2.4	13	20.0	30.6	24.2 ± 2.7	4	18.7	26.0	22.9 ± 3.1	2	16.5	17.0	16.8 ± 0.4
Ear length	19	11.2	17.5	14.9 ± 2.2	12	11.6	15.4	13.4 ± 1.6	5	8.4	12.7	10.3 ± 1.9	2	6.9	7.1	7.0 ± 0.1
Ear width	19	8.2	12.7	10.5 ± 1.1	12	7.2	10.9	9.9 ± 1.1	5	5.8	9.9	7.9 ± 1.7	2	5.1	5.2	5.2 ± 0.1
Nasal Stripe length	19	9.5	19.4	13.0 ± 2.4	13	8.2	15.1	11.8 ± 1.9	5	8.9	12.5	11.3 ± 2.7	-	NA	NA	NA
Nasal Stripe width	19	3.9	4.6	4.1 ± 0.2	13	3.5	4.5	4.0 ± 0.2	5	3.5	3.8	3.8 ± 0.4	-	NA	NA	NA
Eye diameter	21	7.2	9.7	8.3 ± 0.6	14	5.9	8.2	7.2 ± 09	5	5.3	7.8	6.7 ± 1.0	2	3.0	3.0	3.0 ± 0.0
Canine length	17	1.3	2.5	1.9 ± 0.4	14	1.2	2.3	1.6 ± 0.3	2	1.2	1.4	1.3 ± 0.1	-	NA	NA	NA
Internarial distance	21	1.5	2.4	1.8 ± 0.3	14	0.9	1.9	1.5 ± 0.3	5	0.7	1.3	1.1 ± 0.3	-	NA	NA	NA
Tail length / head length	18	2.76	4.06	3.53 ± 0.3	13	3.13	3.97	3.59 ± 0.3	4	2.37	3.69	2.8 ± 0.6	2	2.94	3.25	3.1 ± 0.2
Tail length / head width	18	4.14	7.05	5.4 ± 0.7	13	4.31	6.05	5.33 ± 0.5	4	3.33	5.53	4.36 ± 1.2	2	3.58	3.82	3.70 ± 0.2
Humerus length	17	20.3	26.4	23.2 ± 2.6	12	18.1	26.0	21.0 ± 2.3	2	15.8	21.2	18.5 ± 3.8	-	NA	NA	NA
Radius length	17	20.5	24.7	23.0 ± 1.3	12	20.0	23.1	21.9 ± 0.9	2	16.9	19.0	17.9 ± 1.4	-	NA	NA	NA
Femur length	17	27.0	44.2	34.3 ± 5.1	12	24.8	37.4	30.9 ± 4.7	2	23.6	30.4	27.0 ± 4.8	-	NA	NA	NA
Tibia Length	17	20.0	36.2	30.2 ± 4.5	12	22.3	38.1	27.8 ± 4.5	2	23.2	28.7	25.9 ± 3.9	-	NA	NA	NA
Foot Length	21	22.1	29.4	26.0 ± 2.1	14	18.8	26.4	23.0 ± 1.7	5	16.7	29.1	21.8 ± 5.2	2	15.1	16.3	15.7 ± 0.8
Foot width	17	7.3	10.3	8.5 ± 0.8	12	7.3	10.0	8.2 ± 1.0	2	8.5	10.6	8.5 ± 0.1	-	NA	NA	NA
Longest toe	17	7.3	13.7	12.1 ± 1.7	12	7.2	12.6	10.6 ± 1.4	2	10.2	11.4	10.8 ± 0.8	-	NA	NA	NA
Hand length	17	17.2	23.2	19.7 ± 2.5	12	14.8	21.2	18.5 ± 1.8	2	18.1	19.2	18.6 ± 0.8	-	NA	NA	NA
Hand width	17	6.7	9.8	7.9 ± 0.8	12	5.8	8.3	7.1 ± 0.7	2	6.4	7.4	6.9 ± 0.7	-	NA	NA	NA
Longest finger	17	11.0	13.6	12.7 ± 0.8	12	9.7	13.0	11.5 ± 0.9	2	11.4	12.4	11.9 ± 0.7	-	NA	NA	NA
Intermembranal Index	29*	60.4	86.8	72.5 ± 6.1	-	-	-	-	-	-	-	-	-	NA	NA	NA
Crural Index	29*	60.12	129.4	91.7 ± 24.5	-	-	-	-	-	-	-	-	-	NA	NA	NA
Brachial Index	29*	82.4	122.3	102.1 ± 10.3	-	-	-	-	-	-	-	-	-	NA	NA	NA

Table 3b.

Complete biometric analysis of the ten *M. tanosi* captured at Nahampoana Private Reserve in May 2019. Age classes based on the description in Groves & Harding (2003) and assessment made in the field based on weight class. *Indicates combined adult and sub-adult individuals.

Locality	Nahampoana (n=10)														
	Adult				Sub-adult				Juvenile				Infant		
	n	Min	Max	Mean ± SD	*n*	Min	Max	Mean ± SD	*n*	Min	Max	Mean ± SD	*n*	Min	Max	Mean ± SD
Body mass (sexes combined)	3	63.0	73.6	66.4 ± 6.3	5	41.5	56.0	48.9 ± 5.2	2	29.0	36.0	32.5 ± 4/9	-	NA	NA	NA
Body mass (female)	2	63.0	73.6	68.3 ± 7.5	5	41.5	56.0	48.9 ± 5.2	2	29.0	36.0	32.5 ± 4/9	-	NA	NA	NA
Body mass (male)	1	62.4	62.4	62.4 ± 0.0	-	NA	NA	NA	-	NA	NA	NA	-	NA	NA	NA
Body mass index (sexes combined)	3	3.230	4.864	4.110 ± 0.8	5	3.390	5.060	3.970 ± 0.7	2	2.193	3.989	3.091 ± 1.3	-	NA	NA	NA
Body mass index (female)	2	4.233	4.865	4.549 ± 0.4	5	3.390	5.060	3.970 ± 0.7	2	2.193	3.989	3.091 ± 1.3	-	NA	NA	NA
Body mass index (male)	1	3.230	3.230	3.230 ± 0.0	-	NA	NA	NA	-	NA	NA	NA	-	NA	NA	NA
Head and body length (sexes combined)	3	122.0	139.0	128.0 ± 9.5	5	100.0	121.0	111.6 ± 8.5	2.0	95.0	115.0	105 ± 14.1	-	NA	NA	NA
Head and body length (female)	2	122.0	123.0	122.5 ± 0.7	5	100.0	121.0	111.6 ± 8.5	2.0	95.0	115.0	105 ± 14.1	-	NA	NA	NA
Head and body length (male)	1	139.0	139.0	139.0 ± 0.0	-	NA	NA	NA	-	NA	NA	NA	-	NA	NA	NA
Tail length (sexes combined)	3	120.0	145.0	133.7 ± 12.7	5	110.0	123.0	118.6 ± 6.2	2	122.0	126.0	124.0 ± 2.8	-	NA	NA	NA
Tail length (female)	2	120.0	145.0	132.5 ± 17.7	5	110.0	123.0	118.6 ± 6.2	2	122.0	126.0	124.0 ± 2.8	-	NA	NA	NA
Tail length (male)	1	136.0	136.0	136.0 ± 0.0	-	NA	NA	NA	-	NA	NA	NA	-	NA	NA	NA
Tail width (sexes combined)	3	8.3	10.7	9.6 ± 1.2	5	5.9	7.5	7.1 ± 0.7	2	4.5	7.3	5.9 ± 2.0	-	NA	NA	NA
Tail width (females)	2	9.7	10.7	10.2 ± 0.7	5	5.9	7.5	7.1 ± 0.7	2	4.5	7.3	5.9 ± 2.0	-	NA	NA	NA
Tail width (males)	1	8.3	8.3	8.3 ± 0.0	-	NA	NA	NA	-	NA	NA	NA	-	NA	NA	NA
Total length (sexes combined)	3	242.0	275.0	261.7 ± 17.4	5	214.0	242.0	230.2 ± 10.1	2	217.0	241.0	229.0 ± 17.0	-	NA	NA	NA
Total length (female)	2	242.0	268.0	255.0 ± 18.4	5	214.0	242.0	230.2 ± 10.1	2	217.0	241.0	229.0 ± 17.0	-	NA	NA	NA
Total length (male)	1	275.0	275.0	275.0 ± 0.0	-	NA	NA	NA	-	NA	NA	NA	-	NA	NA	NA
Dorsal stripe length	3	89.00	102.00	97.3 ± 7.2	5	69.00	86.00	78.6 ± 6.9	2	52.00	78.20	65.1 ± 18.6	-	NA	NA	NA
Dorsal stripe width	3	3.8	7.4	5.9 ± 1.9	5	5.0	6.2	5.5 ± 0.5	2	4.5	5.3	4.8 ± 0.5	-	NA	NA	NA
Head length	3	35.2	39.3	36.9 ± 2.2	5	31.9	39.9	34.9 ± 3.6	2	30.0	36.9	33.5 ± 4.9	-	NA	NA	NA
Head width	3	20.4	24.8	22.7 ± 2.2	5	19.2	23.4	21.5 ± 2.1	2	19.0	25.3	22.1 ± 4.4	-	NA	NA	NA
Ear length	3	9.8	14.7	12.1 2.5	5	11.3	15.3	13.0 1.5	2	10.1	12.8	11.5 ± 1.9	-	NA	NA	NA
Ear width	3	7.7	11.2	9.5 ± 1.7	5	9.1	12.1	10.8 ± 1.5	2	7.2	1.0	8.6 ± 1.9	-	NA	NA	NA
Nasal Stripe length	3	10.9	12.5	11.9 ± 0.8	5	8.8	16.9	11.0 ± 3.4	2	10.0	12.4	11.2 ± 1.7	-	NA	NA	NA
Nasal Stripe width	3	3.6	3.9	3.7 ± 0.2	5	2.9	5.4	3.7 ± 1.0	2	3.2	3.6	3.4 ± 0.3	-	NA	NA	NA
Eye diameter	3	6.8	7.2	7.0 ± 0.2	5	5.1	6.9	6.0 ± 0.9	2	3.9	5.4	4.5 ± 1.0	-	NA	NA	NA
Canine length	3	1.6	1.8	1.7 ± 0.1	5	0.8	2.0	1.4 ± 0.1	2	1.3	1.4	1.3 ± 0.1	-	NA	NA	NA
Internarial distance	3	1.5	1.8	1.7 ± 0.2	5	1.0	1.9	1.6 ± 0.3	2	1.3	1.4	1.4 ± 0.1	-	NA	NA	NA
Tail length / head length	3	3.40	3.77	3.62 ± 0.2	5	2.93	3.85	3.43 ± 0.4	2	3.41	4.07	3.74 ± 0.5	-	NA	NA	NA
Tail length / head width	3	4.84	6.67	5.95 ± 1.0	5	4.64	6.39	5.56 ± 0.7	2	4.98	6.42	5.70 ± 1.1	-	NA	NA	NA
Humerus length	3	18.3	27.1	23.0 ± 4.4	5	18.9	26.0	21.8 ± 2.7	2	20.5	22.0	21.3 ± 1.0	-	NA	NA	NA
Radius length	3	18.3	22.9	23.6 ± 3.4	5	18.4	25.0	22.5 ± 2.7	2	19.5	20.5	20.0 ± 1.4	-	NA	NA	NA
Femur length	3	27.4	31.5	29.5 ± 2.1	5	23.5	31.8	29.2 ± 3.8	2	28.2	29.1	28.68 ± 0.6	-	NA	NA	NA
Tibia Length	3	25.6	32.0	28.5 ± 3.2	5	17.0	31.5	23.9 ± 5.3	2	20.4	27.9	24.2 ± 5.3	-	NA	NA	NA
Foot Length	3	23.6	23.9	23.8 ± 0.2	5	21.6	24.5	22.7 ± 1.2	2	18.6	23.4	21.0 ± 3.4	-	NA	NA	NA
Foot width	3	8.8	10.1	9.6 ± 0.7	5	9.4	10.3	9.8 ± 0.4	2	8.1	9.7	8.9 ± 1.1	-	NA	NA	NA
Longest toe	3	10.6	12.6	11.6 ± 1.2	5	10.6	13.0	11.3 ± 1.0	2	11.0	11.3	11.1 ± 0.2	-	NA	NA	NA
Hand length	3	21.3	22.8	22.1 ± 0.8	5	17.6	21.6	19.3 ± 1.6	2	19.1	19.8	19.4 ± 0.5	-	NA	NA	NA
Hand width	3	6.6	8.7	7.7 ± 1.1	5	7.2	8.3	7.7 ± 0.4	2	6.8	7.6	7.2 ± 0.6	-	NA	NA	NA
Longest finger	3	10.5	13.6	12.5 ± 1.7	5	7.8	13.0	10.5 ± 2.2	2	10.4	11.8	11.1 ± 1.0	-	NA	NA	NA
Intermembranal Index	8*	62.9	98.3	81.1 ± 10.2	-	-	-	-	-	-	-	-	-	NA	NA	NA
Crural Index	8*	60.7	136.2	90.9 ± 22.7	-	-	-	-	-	-	-	-	-	NA	NA	NA
Brachial Index	8*	73.1	113.0	95.9 ± 12.9	-	-	-	-	-	-	-	-	-	NA	NA	NA

Phenotypic variation

To accompany the biometric data presented in **Chapter 3** (and see **Appendix**; **Tables 3a+3b**), a series of photographs are presented for comparison of general phenotype (**Plate 1**). Examination of the images revealed a few noteworthy characteristics that appear to show some variation between individuals and perhaps may be limited to certain sub-populations. Firstly, the striking image of an adult individual from the northern most Lost Rainforest site (**Plate 1**, **I**) with green eyes shows an obvious but rare characteristic, although it has also been observed in a small number of individuals from Sainte Luce. The great majority of individuals captured in this study have brown iris pigmentation. Furthermore, a small number of individuals (n=3) captured in Ivolo and Enato by A. Hapke and N. Andrianjaka show distinctive black tail tips (**Plate 1**, **L**), which has neither been seen or reported elsewhere. In one particular individual the dark colouration entends distally half way down the tail. This has not been seen in the population in Sainte Luce, the most extensively sampled sub-population of *M. tanosi* to date. The outward appearance of the sub-population of *M. tanosi* in Sainte Luce closely matches the phenotype provided in the original species description by Rasoloarison et al, 2013 (see **Chapter 2; Study species**). Examination of individuals captured at Nahampoana Private Reserve revealed a distinctive difference in pelage colouration from the more familiar individuals from Sainte Luce. Individuals captured at this locality (n=10), generally appear more grey in colouration. Following the same descriptive process as Rasoloarison et al (2013) and utilising the same standardised colour palettes (Smithe, 1974), I hereby characterise the sub-population of *M. tanosi* observed at Nahampoana Private Reserve with colouration observed under natural light.

The dense and dark dorsal hairs are bicoloured, resulting in a blend of Cinnamon (123A) and Drab-Gray (119D) in most individuals. Guard hairs are mostly pale and white. The dorsal stripe, when visible varies from Fawn Color (25) to Burnt Umber (22) and is diffused. As described from the type specimen, ventral fur has a soft grayish-beige fur along the central and upper portions of the belly and bicolored dull beige and Pale Neutral Gray (86) flanks. The underfur of the dorsum surface is Dark Neutral Gray (83) and Light Neutral Gray (85) on the ventrum. Ears are Fawn Color (25) and crown colouration varies between Buff (24) and Cinnamon (39). Supra-ocular colouration varies between Buff (24) and Clay Color (26), gradating to a pale golden Straw Yellow (56) in buccal areas. The face has a uniform pale nasal stripe above the nose and between the eyes and diffuses into the crown. The dense and long hairs on the tail are of similar colouration to those that constitute the dorsal dark stripe, varying from Fawn Color (25) to Antique Brown (37) on the dorsal surface to Buff (24) on the ventral side. The upper surfaces of hands and hind

feet are Chamois (123D), and forearms show a similar colouration to the crown (Buff 24 & Cinnamon 39). Vibrissae are dark. However, some individuals in the Nahampoana population also showed highly unusual colouration (**Plate 1**, **H**). Such individuals show a distinctly grey dorsal pelage, with bicolour hairs of Pale Neutral Gray (86) and pale whitish guard hairs on the upper back, gradating to a pale Buff (24) on the lower back (pelvic region) and extending down the tail. The diffused dorsal stripe varies from Tawny Olive (223D) Olive Brown (28).

Despite the close match between the original description and individuals from Sainte Luce, the phenotype notably exhibits a distinctive Ferruginous (41) colouration around the eyes, on the crown and also in patches on the dorsal surface of the forearm. Infant *M. tanosi* in Sainte Luce differ from the older and more developed individuals (**Plate 1**, **D**). Dorsal pelage in observed infants is a mix of Drab (27), Smoke Gray (45) and cinnamon (39) whilst the prominent crown and facial colouration is lacking and is similar to that of the dorsal hair. The dense long cover hairs are light in colouration, and vibrissae are dark as in adults. Ears are Sayal Brown (223C). The white nasal stripe is visible but not as distinct as in older individuals and is a similar colour to the soft greyish-beige fur that covers the ventral surface.

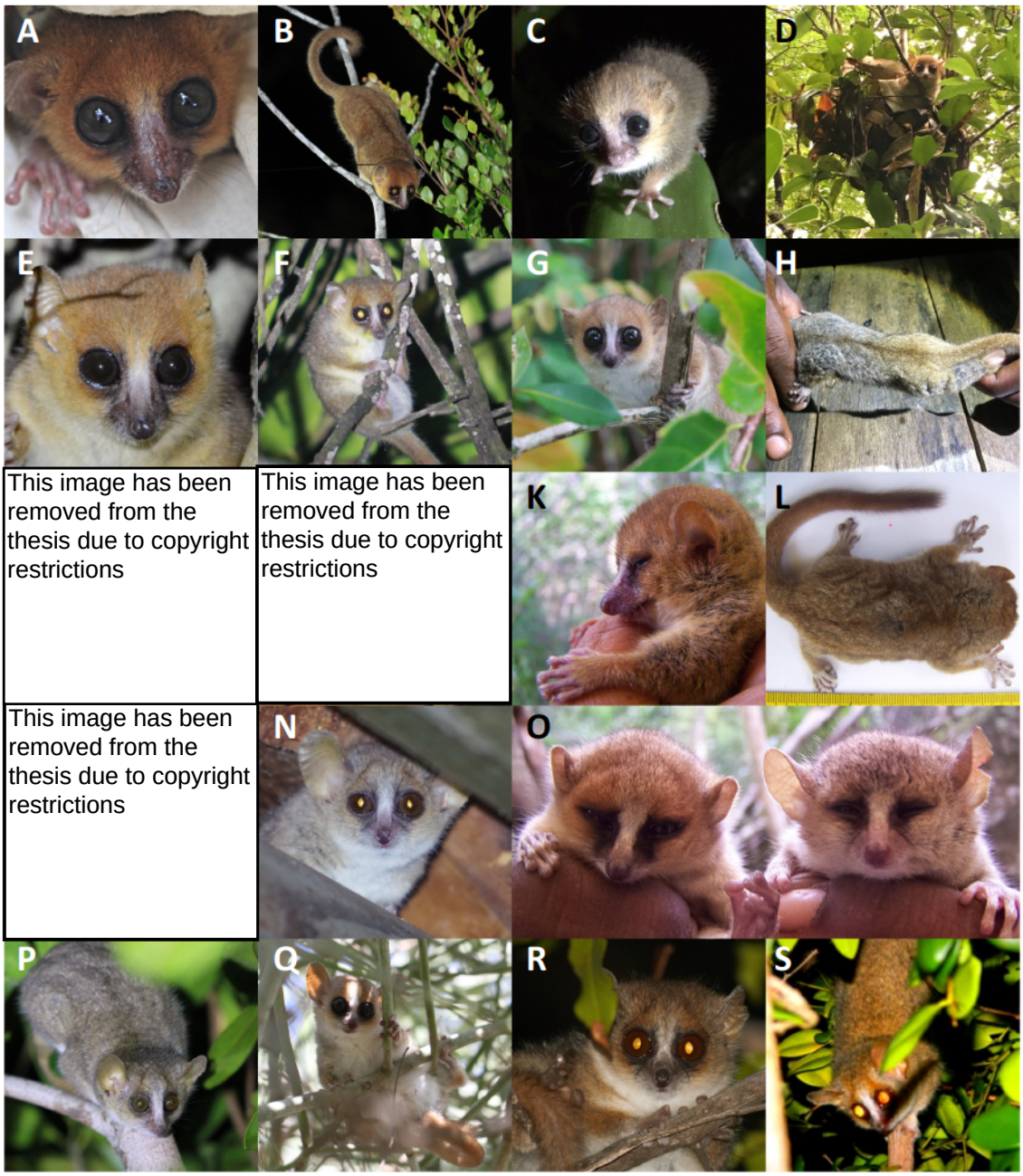


Plate 1 – The *Microcebus* spp. of southeast Madagascar according to present knowledge. The plate provides photographic examples of *M. tanosi* individuals across its known range and also shows the phentotypic variation across the 6 representative species. **A-D)** *Microcebus tanosi* from the littoral forests of Sainte Luce; **A)** Adult facial colouration and pattern, note relatively small ears. **B**) dorsal view of a radio-collared adult male displaying dark dorsal stripe. **C**) Vigilant adult female in typical leaf next. **D**) Infant observed away from nest. **E-H**) *Microcebus tanosi* from Nahampoana Private Reserve; **E**) Facial colouration and pattern of adult male. **F**) Adult male ventral view. **G**) An additional image showing pelage colour in day light. **H**) Dorsal view showing distinctive grey dorsal pelage common in individuals from this population. **I-J**) *Microcebus tanosi* from the Lost Rainforest; **I**) Facial colouration and unusual green eye colour. **J**) Dorsal view showing clear dark dorsal stripe. **K**) *Microcebus tanosi* from Mahamavo rainforest;

lateral view of sedated individual, showing typical small ears. **L**) A fully sedated individual from Ivolo, showing a distinct dorsal stripe and unusual black tail. **M**) *Microcebus tanosi* from the rainforest at Ampasy. **N**) A side by side comparison of *M. tanosi* and a species identified as *Microcebus murinus* at Andohahela National Park (Mahamavo). Although lighting does not show colouration well, ear morphology is distinctive. **O**) *Microcebus ganzhorni* from the species' type locality, the littoral forests of Mandena. Note large ears and grey facial pelage. **P**) *Microcebus ganzhorni* from the littoral forests of Mandena (Lokaro). **Q**) *Microcebus griseorufus* from the spiny forest near Berenty. **R**) *Microcebus manitatra* from the forests of Ambatosirongorongo mountain. **S**) *Microcebus* sp. from the littoral forests of Petriky. All photographs by SHR except for **I+J** Noel Rowe, **K**, **L+N** Jacques Rakotondranary, **M** Kai Schütte, **O** Elena Račevska, **R+S** Giuseppe Donati.

A description of the constructed leaf nests of *M. tanosi* in the littoral forests of Sainte Luce.

The structure of the leaf nests observed in Sainte Luce were approximately spherical in shape, and similar to those described by Atsalis (2008) used by *M. rufus* in Ranomafana National Park. Composition varied in terms of the tree species used, but predominantly consisted of around 100 or so tightly inter-wound leaves (see **Chapter 5**, **Fig 4 A**), with a small concealed aperture, roughly 4cm in diameter for entry and egress. Similar to the observations made by Atsalis (2008), nests were not always well concealed, and were found on average to be positioned in areas of less dense forest compared to sleeping sites, but in denser areas than at random points in the surrounding forest. The average height of leaf nests was found to be 3.8m (min=1.5m, max=7m) and were often constructed around and supported by thin branches. The position of the nests has been posited as being defensive in nature (Atsalis, 2008), even if security from predators is not the structures primary function (Fruth & McGrew, 1998). With some nests constructed around thin, distal branches any slight approach from a would-be predator could be detected by lemurs inside the nest. The construction of leaf nests has been proposed as an ancestral strepsirrhine trait (Martin, 1972) however, it is apparent that not all mouse lemur species employ the strategy. The separation hints at a phylogenetic based division between species pertaining to the adaptive behaviours concerning sleep related ecology. No nests were observed during construction, so it remains unclear which sex is responsible for their creation.

Table 4.

A comparison of home range overlap (area) between all Sainte Luce study individuals for both the adjusted core MCP and 95% fixed kernel analysis.

Overlap matrix - Adjusted MCP's (Ha)

Lemur ID	ML1 F	ML2 F	ML3 F	ML4 F	ML5 F	ML6 F	ML7 F	ML8 F	ML9 M	ML10 M	ML11 M	ML12 M	ML13 M
ML1 F (2.0ha)		X	X	1.92	X	0.21	X	X	X	0.90	1.62	X	0.73
ML2 F (1.1ha)	X		0.77	X	X	X	X	X	X	1.11	1.09	X	X
ML3 F (0.9ha)	X	0.77		X	X	X	X	X	X	0.94	0.85	X	X
ML4 F (8.3ha)	1.92	X	X		X	0.12	X	X	1.30	1.48	2.74	X	0.86
ML5 F (3.8ha)	X	X	X	X		0.02	X	X	X	X	X	X	0.47
ML6 F (2.7ha)	0.21	X	X	0.12	0.02		X	X	X	X	0.07	X	0.78
ML7 F (1.5ha)	X	X	X	X	X	X		X	X	X	X	0	1.15
ML8 F 3.6ha)	X	X	X	X	X	X	X		X	X	X	X	X
ML9 M (5.2ha)	X	X	X	1.30	X	X	X	X		0.04	0.91	X	X
ML10 M (10.0ha)	0.90	1.11	0.94	1.48	X	X	X	X	0.04		4.24	0.31	0.04
ML11 M (16.5ha)	1.62	1.09	0.85	2.74	X	0.07	X	X	0.91	4.24		0.42	0.88
ML12 M (6.3ha)	X	X	X	X	X	X	0.00	X	X	0.31	0.42		X
ML13 M (6.1ha)	0.73	X	X	0.86	0.47	0.78	1.15	X	X	0.04	0.88	X	

Overlap matrix - Adjusted 95% Fixed Kernals (Ha)

Lemur ID	ML1 F	ML2 F	ML3 F	ML4 F	ML5 F	ML6 F	ML7 F	ML8 F	ML9 M	ML10 M	ML11 M	ML12 M	ML13 M
ML1 F (2.0ha)		X	X	0.55	X	0.14	X	X	X	0.61	1.20	X	0.20
ML2 F (1.1ha)	X		0.24	X	X	X	X	X	X	0.04	0.40	X	X
ML3 F (0.9ha)	X	0.24		X	X	X	X	X	X	0.50	0.41	X	X
ML4 F (8.3ha)	0.55	X	X		0.00	0.33	0.10	X	0.99	0.63	2.00	X	1.31
ML5 F (3.8ha)	X	X	X	0.00		0.12	X	X	X	X	X	X	0.22
ML6 F (2.7ha)	0.14	X	X	0.33	0.12		X	X	X	X	0.22	X	0.63
ML7 F (1.5ha)	X	X	X	0.10	X	X		X	X	X	0.00	0.00	0.90
ML8 F 3.6ha)	X	X	X	X	X	X	X		X	X	X	X	X
ML9 M (5.2ha)	X	X	X	0.99	X	X	X	X		X	0.26	X	X
ML10 M (10.0ha)	0.61	0.04	0.50	0.63	X	X	X	X	X		3.60	0.13	0.10
ML11 M (16.5ha)	1.20	0.40	0.41	2.00	X	0.22	0.00	X	0.26	3.60		0.10	1.12
ML12 M (6.3ha)	X	X	X	X	X	X	0.00	X	X	0.13	0.10		X
ML13 M (6.1ha)	0.20	X	X	1.31	0.22	0.63	0.90	X	X	0.10	1.12	X	

Table 5a.

Population descriptives for the three nocturnal lemur species in the largest forest fragment in the study, 'S9' between 2011 and 2018. The fragment has been formally protected since 2015. Results are based on pooled two-year datasets, increasing the number of observations and improving estimate accuracy. The reduced effort attributed to *C. thomasi* is a result of the exclusion of transects conducted during the winter period (May-Sept), when the species undergoes hibernation.

Descriptive parameters of the nocturnal lemur populations of Sainte Luce. S9. 346Ha.

Species	Year	*Total Effort (m)*	*n*	*N*	*N LCI*	*N UCI*	N_s	$E_{(s)}$	*D / Ha*	D_s / *Ha*	*EnR / km)*	P_a	*GOF-KS p*	*Model*
Avahi meridionalis	2011-2012	89,051	572	770	406	1598	438	1.74	2.226	1.282	3.62	0.53	0.853	Hazard Rate + Single Polynomial +2% +PS
	2013-2014	35,277	125	422	218	818	253	1.65	1.221	0.739	2.07	0.49	0.904	Hazard Rate + Single Polynomial + 2% +PS
	2015-2016	32,566	109	519	244	1107	319	1.49	1.501	1.011	2.95	0.62	0.575	Half Normal + COS +PS
	2017-2018	30,568	104	361	224	583	249	1.40	1.043	0.743	2.32	0.52	0.960	Hazard Rate + Single Polynomial +2% +PS
Cheirogaleus thomasi	2011-2012	44,212	115	478	361	635	–	–	1.383	–	2.60	0.38	0.631	Hazard Rate + Single Polynomial + PS
	2013-2014	23,846	55	398	201	785	–	–	1.149	–	2.31	0.52	0.967	Hazard Rate + Single Polynomial + PS
	2015-2016	14,784	43	427	238	765	–	–	1.268	–	2.91	0.45	0.547	Hazrad Rate + Single Polynomial + PS
	2017-2018	17,735	41	432	206	904	–	–	1.247	–	2.31	0.55	0.947	Hazard Rate + Single Polynomial
Microcebus tanosi	2011-2012	89,051	60	151	108	211	–	–	0.436	–	0.61	0.56	0.959	Half Normal + COS + 10%
	2013-2014	35,277	34	159	119	213	–	–	0.460	–	0.94	0.73	0.990	Hazard Rate + Single Polynomial + 2%
	2015-2016	32,566	27	266	148	478	–	–	0.769	–	1.15	0.61	0.994	Half Normal + COS +2.5% + PS
	2017-2018	30,568	25	131	70	246	–	–	0.379	–	0.79	0.55	0.924	Half Normal + COS +2.5%

Table 5b.

Population descriptives for the three nocturnal lemur species in 'S7' between 2011 and 2018. The fragment was designated a community resource zone (CRZ) in 2015 and has since experienced severe degradation. Results are based on pooled two-year datasets. The reduced effort attributed to *C. thomasi* is the result of excluded winter transects (May-Sept), when the species undergoes hibernation. * Signifies a very low number of observations. *** indicates too few observations for reliable Distance output.

Descriptive parameters of the nocturnal lemur populations of Sainte Luce. S7. 224Ha.

Species	Year	*Total Effort (m)*	*n*	*N*	*N LCI*	*N UCI*	N_s	$E_{6)}$	*D / Ha*	D_s / *Ha*	*EnR / km)*	P_a	*GOF-KS p*	*Model*
Avahi meridionalis	2011-2012	1,800	0	***	–	–	–	–	–	–	–	–	–	–
	2013-2014	15,897	4*	***	–	–	–	–	–	–	0.13	–	–	–
	2015-2016	7,829	1*	***	–	–	–	–	–	–	0.13	–	–	–
	2017-2018	14,496	0	***	–	–	–	–	–	–	–	–	–	–
Cheirogaleus thomasi	2011-2012	1,800	7*	382*	336	434	–	–	1.706	–	3.89	1.00	0.734	Hazard Rate + Single Polynomial + 2.5%
	2013-2014	10,682	45	455	301	687	–	–	2.030	–	4.21	0.32	0.933	Half Normal + COS
	2015-2016	5,545	27	296	200	438	–	–	1.322	–	4.51	0.97	0.927	Hazard Rate + Single Polynomial + 6%
	2017-2018	10,142	70	490	374	644	–	–	2.189	–	6.70	0.40	0.968	Hazard Rate + Single Polynomial + 2.5%
Microcebus tanosi	2011-2012	1,800	0	***	–	–	–	–	–	–	–	–	–	–
	2013-2014	15,897	6*	30*	12	75	–	–	0.136	–	0.38	0.63	0.483	Half Normal + COS
	2015-2016	7,829	3*	25*	3	217	–	–	0.114	–	0.38	1.00	0.540	Half Normal + COS
	2017-2018	14,496	3*	28*	5	148	–	–	0.129	–	0.21	1.00	0.893	Half Normal + COS

Table 5c.

Population descriptives for the three nocturnal lemur species in forest fragment 'S8' between 2011 and 2018. The fragment is divided by a road into a northern and a southern portion, which vary in both size and condition and are therefore analysed separately. Results are based on pooled two-year datasets. The reduced effort attributed to *C. thomasi* is the result of excluded winter transects (May-Sept), when the species undergoes hibernation. * Signifies a very low number of observations. *** indicates that too few observations were made to produce a reliable series of descriptive results.

Descriptive parameters of the nocturnal lemur populations of Sainte Luce. S8. 50.9Ha. (N+S pooled).

Species	Section	Year	al Effort (	n	N	N LCI	N UCI	N_s	$E_{(\theta)}$	D / Ha	D_s / Ha	EnR / km)	P_a	GOF-KS p	Model
Avahi meridionalis	S8N	2011-2012	9,924	28	66	43	101	40	1.75	1.622	0.928	2.72	0.56	0.935	Half Normal + COS + 5%
	S8S	2011-2012	3,535	5*	8	2	29	4	1.62	0.768	0.787	1.41	0.77	0.910	Half Normal + COS + 5% (Strat)
	Pooled	2011-2012	13,459	33	65	40	106	38	1.67	1.273	0.764	2.30	0.78	0.944	Half Normal + COS + 5%
	S8N	2013-2014	7,607	7*	20	5	84	10	2.03	0.486	0.240	0.92	0.75	0.709	Half Normal + COS + 5% (Strat)
	S8S	2013-2014	2,915	6*	11	0	256	8	1.16	1.061	0.912	2.06	0.44	0.888	Half Normal + COS + 5% (Strat)
	Pooled	2013-2014	10,522	14	30	9	99	17	1.44	0.585	0.405	1.24	0.60	0.909	Half Normal + COS + 5%
	S8N	2015-2016	17,808	17	19	9	40	10	1.51	0.475	0.314	0.95	0.92	0.902	Half Normal + COS + 2.5% (Strat)
	S8S	2015-2016	8,238	22	28	9	84	15	2.13	2.654	1.244	2.67	0.68	0.892	Hazard Rate + Single Polynomial
	Pooled	2015-2016	26,046	40	52	24	117	21	1.82	1.031	0.567	1.50	0.80	0.955	Half Normal + COS + 2.5%
	S8N	2017-2018	9,013	13	29	10	87	23	1.15	0.713	0.620	1.14	0.58	0.952	Hazard Rate + SP
	S8S	2017-2018	6,356	15	14	6	30	8	1.56	1.321	0.848	2.36	0.88	0.628	Half Normal + COS
	Pooled	2017-2018	15,369	28	46	27	79	31	1.34	0.910	0.680	1.69	0.86	0.696	Half Normal + COS + 6%
Cheirogaleus thomasi	S8N	2011-2012	4,735	26	103	46	233	–	–	2.550	–	5.49	0.62	0.816	Hazard Rate + Single Polynomial (Strat)
	S8S	2011-2012	2,414	9*	30	5	162	–	–	2.862	–	2.41	0.37	0.920	Hazard Rate + Single Polynomial (Strat)
	Pooled	2011-2012	7,149	35	132	61	286	–	–	2.601	–	4.90	0.54	0.620	Hazard Rate + Single Polynomial
	S8N	2013-2014	3,213	19	117	68	199	–	–	2.880	–	5.91	0.43	0.753	Hazard Rate + Single Polynomial (Strat)
	S8S	2013-2014	2,201	10	17	7	42	–	–	1.603	–	4.54	0.61	0.292	Hazard Rate + Single Polynomial (Strat)
	Pooled	2013-2014	5,414	29	118	80	173	–	–	2.312	–	5.36	0.49	0.610	Half Normal + COS
	S8N	2015-2016	10,200	38	77	35	169	–	–	1.907	–	3.73	0.40	0.934	Hazard Rate + Single Polynomial + 3% (Strat)
	S8S	2015-2016	3,575	14	17	5	53	–	–	1.602	–	3.92	0.50	0.932	Hazard Rate + Single Polynomial + 3% (Strat)
	Pooled	2015-2016	13,775	52	81	50	132	–	–	1.594	–	3.78	0.40	0.960	Hazard Rate + Single Polynomial + 3%
	S8N	2017-2018	5,125	16	157	46	534	–	–	3.876	–	5.46	0.62	0.996	Half Normal + COS +2.5% (Strat) + PS
	S8S	2017-2018	3,535	28	42	22	83	–	–	4.079	–	4.53	0.49	0.995	Half Normal + COS +2.5% (Strat)
	Pooled	2017-2018	8,660	44	199	102	389	–	–	3.919	–	5.08	0.57	0.926	Half Normal + COS +2.5%
Microcebus tanosi	S8N	2011-2012	9,924	3*	***	–	–	–	–	–	–	0.30	–	NA	–
	S8S	2011-2012	3,535	4*	***	–	–	–	–	–	–	0.11	–	NA	–
	Pooled	2011-2012	13,459	7*	***	–	–	–	–	–	–	0.48	–	NA	–
	S8N	2013-2014	7,607	3*	***	–	–	–	–	–	–	0.39	–	NA	–
	S8S	2013-2014	2,915	3*	***	–	–	–	–	–	–	0.10	–	NA	–
	Pooled	2013-2014	10,522	6*	***	–	–	–	–	–	–	0.57	–	NA	–
	S8N	2015-2016	17,808	7*	14	6	34	–	–	0.337	–	0.39	0.65	NA	Half Normal + COS + Manual CP
	S8S	2015-2016	8,238	0*	***	–	–	–	–	–	–	0.00	–	NA	–
	Pooled	2015-2016	26,046	7*	***	–	–	–	–	–	–	0.27	–	NA	–
	S8N	2017-2018	9,013	5*	12	1	121	–	–	0.292	–	0.55	0.47	NA	Half Normal + COS + Manual CP +PS
	S8S	2017-2018	6,356	1*	***	–	–	–	–	–	–	0.16	–	NA	–
	Pooled	2017-2018	15,369	6*	12	2	63	–	–	0.227	–	0.39	0.43	NA	Half Normal + COS + Manual CP

Species Inventories (Sainte Luce):

IUCN categories: Data Deficient (DD), Not Assessed (NA), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW) and Extinct (EX).

Table 6a. Mammals

Mammalian species occupying the littoral habitats of Sainte Luce. Microbat fauna based on Jenkins et al, 2007. *Represents a species whose taxonomic identity needs further study.

Order	Family	Species	IUCN Status
Primates	Indriidae	*Avahi meridionalis*	EN
	Cheirogaleidae	*Cheirogaleus thomasi*	CR
		Microcebus tanosi	EN
	Lemuridae	*Eulemur collaris*	EN
Carnivora	Eupleridae	*Fossa fossana*	VU
Rodentia	Nesomyidae	*Elirurus webbi*	LC
	Muridae	*Rattus rattus*	LC
Eulipotyphla	Soricidae	*Suncus etruscus*	LC
		Suncus murinus	LC
Afrosoricidae	Tenrecidae	*Tenrec ecaudatus*	LC
		Setifer setosus	LC
		Oryzorictes hova	LC
Chiroptera	Pteropodidae	*Pteropus rufus*	VU
	Hipposideridae	*Hipposideridae* sp. nov	NA
		Hipposideros commersoni	NT
	Vespertilionidae	*Myotis goudoti*	LC
		Miniopterus majori / fratercula *	
		Scotophilus robustus	LC
		Vespertilionid sp.	NA
	Myzopodidae	*Myzopoda aurita*	LC
	Molossidae	*Tadarida fulminans*	LC
		Molossid sp.1	NA
		Molossid sp.2	NA
Cetartiodactyla	Suidae	*Potamochoerus larvata hova*	LC

Table 6b. Amphibians and Reptiles

Amphibian and reptile species occupying the littoral habitats of Sainte Luce. All species validated using genetic tools (S. Hyde Roberts. unpub. data) except *.

Order	Family	Species	IUCN Status
Anura	Hyperoliidae	*Heterixalus boettgeri*	LC
	Mantellidae	*Aglyptodactylus inguinalis*	LC
		Boophis madagascariensis	LC
		Boophis opisthodon	LC
		Boophis sp. aff. *pauliani*	NA
		Boophis sp. aff. *picturatus*	NA
		Mantidactylus sp. aff. *tricinctus*	NA
		Guibemantis wattersoni	EN
		Blommersia sp. aff. *blommersae*	NA
		Guibemantis diphonus	CR
		Gephyromantis leucocephalus	NT
		Mantidactylus sp. aff. *majori*	NA
		Guibemantis cf. *pulcher*	NA
		Guibemantis annulatus	EN
		Mantidactlyus sp. nov	NA
	Microhylidae	*Anodonthyla nigrigularis*	EN
		Paradoxophyla palmata	LC
		Plethodontohyla alluadi	LC
		Plethodontohyla bipunctata	LC
		Plethodontohyla notosticta	LC
		Mini scule	NA
	Ranidae	*Ptychadena mascareniensis*	LC
Squamata	Boidae	*Acrantophis dumerili*	LC
		Sanzinia madagascariensis	LC
	Chamaleonidae	*Palleon* sp. aff. *nasus*	NA
		Calumma sp. aff. *nasutum*	NA
		Furcifer lateralis	LC
		Furcifer verrucosus	LC
	Pelomedusidae	*Pelomedusa subrufa*	NA
	Chelonidae	*Caretta caretta**	VU
		Chelonia mydas	EN
		*Dermochelys coriacea**	CR
		*Eretmochelys imbricata**	CR
	Crocodylidae	*Crocodilus niloticus**	LC
	Elapidae	*Pelamis platura*	LC
	Gekkonidae	*Ebenavia* sp. aff. *inunguis*	NA
		Geckolepis sp. aff. *maculata*	NA
		Hemidactylus mercatorius	LC
		Lygodactylus sp. aff. *miops*	NA
		Matoatoa spannringi	DD
		Phelsuma antanosy	CR
		Phelsuma lineata	LC
		Phelsuma modesta	LC
		Phelsuma parva	LC
		Uroplatus sikorae	LC

Gerrhosauridae	*Zonosaurus anelanelany**	VU
	Zonosaurus laticaudatus	LC
	Zonosaurus maximus	VU
Iguanidae	*Oplurus quadrimaculatus*	LC
Lamprohphiidae	*Dromicodryas bernieri*	LC
	Ithycyphus goudoti	LC
	Ithychyphus oursi	LC
	Leioheterodon madagascariensis	LC
	Liophidium rhodogaster	LC
	Liophidium torquatum	LC
	Liophidium vaillanti	LC
	Thamnosophis infrasignatus	LC
	Thamnosophis lateralis	LC
	Phisalixella arctifasciata	LC
	Lycodryas gaimardi	LC
	Lycodryas sp. nov	NA
	Madagascarophis meridionalis	LC
	Micropisthodon ochraceus	LC
	Mimophis mahfalensis	LC
	Liophidium cf. *kely*	EN
	Pseudoxyrhopus sp. aff. *tritaeniatus*	NA
	Pseudoxyrhopus sokosoko	VU
Scincidae	*Amphiglossus astrolabi*	LC
	Madascincus sp. aff. *melanopleura*	NA
	Amphiglossus sp. aff. *ornaticeps*	NA
	Amphiglossus spp.*	NA
	Androngo trivittatus	LC
	Trachylepis elegans	LC
	Trachylepis gravenhorstii	LC
Typhlopidae	*Indotyphlops braminus*	NA

Table 6c. Birds

Bird species occupying the littoral habitats of Sainte Luce. Species list is a summation of all known published works (Goodman, 1997; Ellis, 2003; Watson, 2007) and additional surveys conducted by SHR.

Order	Family	Species	IUCN Status
Accipitriformes	Accipitridae	*Accipiter francesiae*	LC
		Accipiter henstii	NT
		Accipiter madagascariensis	NT
		Aviceda madagascariensis	LC
		Buteo brachypterus	LC
		Milvus aegyptus	NR
		Milvus migrans	LC
		Polyboroides radiatus	LC
Anseriformes	Anatidae	*Anas erythrorhyncha*	LC
		Anas melleri	EN
		Dendrocygna viduata	LC
		Nettapus auritus	LC
Apodiformes	Apodidae	*Apus balstoni*	LC
		Apus barbatus	LC
		Cypsiurus parvus	LC
		Tachymarptis melba	LC
		Zoonavena grandidieri	LC
Bucerotiformes	Upupidae	*Upupa marginata*	LC
Caprimulgiformes	Caprimulgidae	*Caprimulgus madagascariensis*	LC
Charadriiformes	Charadriidae	*Charadrius hiaticula*	LC
		Charadrius marginatus	LC
		Charadrius pecuarius	LC
		Charadrius thoracicus	VU
	Glareolidae	*Glareola ocularis*	VU
	Laridae	*Larus dominicanus*	LC
		Sterna bergii	LC
		Sterna caspia	LC
		Sterna dougallii	LC
		Thalasseus bengalensis	LC
	Recurvirostridae	*Himantopus himantopus*	LC
	Rostratulidae	*Rostratula benghalensis*	LC
	Scolopacidae	*Actitis hypoleucos*	LC
		Arenaria interpres	LC
		Calidris alba	LC
		Gallinago macrodactyla	VU
		Numenius phaeopus	LC
		Tringa nebularia	LC
	Turnicidae	*Turnix nigricollis*	LC
Columbiformes	Columbidae	*Alectroenas madagascariensis*	LC
		Nesoenas picturatus	LC
		Oena capensis	LC
		Streptopelia picturata	LC
		Treron australis	LC
Coraciiformes	Alcedinidae	*Corythornis madagascariensis*	LC
		Corythornis vintsioides	LC
	Brachypteraciidae	*Atelornis pittoides*	LC
	Coraciidae	*Eurystomus glaucurus*	LC
	Meropidae	*Merops superciliosus*	LC

Cuculiformes	Cuculidae	*Centropus toulou*	LC
		Coua caerulea	LC
		Coua gigas	LC
		Coua reynaudii	LC
		Cuculus rochii	LC
Falconiformes	Falconidae	*Falco concolor*	VU
		Falco eleonorae	LC
		Falco newtoni	LC
		Falco peregrinus	LC
Galliformes	Phasianidae	*Margaroperdix madagarensis*	LC
	Numididae	*Numida meleagris*	LC
Gruiformes	Rallidae	*Dryolimnas cuvieri*	LC
		Porphyrio madagascariensis	NR
		Porphyrio porphyrio	LC
	Sarothruridae	*Canirallus kioloides*	LC
		Sarothrura insularis	LC
Leptosomiformes	Leptosomidae	*Leptosomus discolor*	LC
Passeriformes	Acrocephalidae	*Acrocephalus newtoni*	LC
		Nesillas typica	LC
	Alaudidae	*Mirafra hova*	LC
	Campephagidae	*Ceblepyris cinereus*	LC
	Cisticolidae	*Cisticola cherina*	LC
		Neomixis striatigula	LC
		Neomixis tenella	LC
		Neomixis viridis	LC
	Corvidae	*Corvus albus*	LC
	Dicruridae	*Dicrurus forficatus*	LC
	Estrildidae	*Lonchura nana*	LC
	Hirundinidae	*Hirundo rustica*	LC
		Phedina borbonica	LC
		Riparia paludicola	LC
	Monarchidae	*Terpsiphone mutata*	LC
	Motacillidae	*Motacilla flaviventris*	LC
	Muscicapidae	*Copsychus albospecularis*	LC
		Saxicola sabila	NR
	Nectariniidae	*Cinnyris notatus*	LC
		Cinnyris sovimanga	LC
	Ploceidae	*Foudia madagascariensis*	LC
		Foudia omissa	LC
	Pycnonotidae	*Hypsipetes madagascariensis*	LC
	Sturnidae	*Acridotheres tristis*	LC
		Hartlaubius auratus	LC
	Vangidae	*Cyanolanius madagascarinus*	LC
		Leptopterus chabert	LC
		Newtonia archboldi	LC
		Newtonia brunneicauda	LC
		Schetba rufa	LC
		Tylas eduardi	LC
		Vanga curvirostris	LC
	Zosteropidae	*Zosterops maderaspatanus*	LC

Pelecaniformes	Ardeidae	*Ardea alba*	LC
		Ardea cinerea	LC
		Ardea purpurea	LC
		Ardeola ralloides	LC
		Bubulcus ibis	LC
		Butorides striata	LC
		Egretta dimorpha	LC
		Ixobrychus minutus	LC
		Nycticorax nycticorax	LC
	Threskiornithidae	*Lophotibis cristata*	NT
	Scopidae	*Scopus umbretta*	LC
Psittaciformes	Psittaculidae	*Agapornis cana*	LC
		Coracopsis nigra	LC
		Coracopsis vasa	LC
Strigiformes	Strigidae	*Asio madagascariensis*	LC
		Athene superciliaris	LC
		Otus rutilus	LC
	Tytonidae	*Tyto alba*	LC
Suliformes	Fregatidae	*Fregata minor*	LC

Table 6d. Insects: Butterflies

Butterfly species occupying the littoral habitats of Sainte Luce. Species inventory compiled by SHR with species identifications validated by Dr. David Lees at the Natural History Museum, London.

Order	Family	Species	IUCN Status
Lepidoptera	Papilionidae	*Pharmocophagus antenor*	NA
		Papilio demodocus	NA
		Papilio epiphorbas	NA
		Papilio oribazus	NA
		Pharmocophagus antenor	NA
	Pieridae:	*Eurema floricola floricola*	NA
		Eurema brigitta pulchella	LC
		Catopsilia thauruma	NA
		Leptosia alcesta sylvicola	NA
		Leptosia nupta viettei	NA
		Appias sabina confusa	NA
		Appias epaphia orbona	NA
		Belenois helcida	NA
	Lycaenidae:	*Spalgis tintinga*	NA
		Hypolycaena philippus ramonza	NA
		Hemiolaus ceres	NA
		Leptomyrina phidias	NA
		Deudorix batidkeli	NA
		Leptotes pirithous	LC
		Leptotes rabefaner	NA
		Euchrysops malathana	NA
		Eicochrysops sanguigutta	NA
		Zizula hylax	NA
		Zizina antanossa	LC
		Zizeeria knysna	LC
		Saribia tepahi	NA
	Nymphalidae:	*Danaus chrysippus orientis*	NA
		Melanitis leda	NA
		Heteropsis narcissus fraterna	NA
		Heteropsis strigula	NA
		Strabena perrieri	NA
		Strabena triophthalma	NA
		Strabena tamatavae	NA
		Charaxes antamboulou	NA
		Charaxes cacuthis	NA
		Salamis anteva	NA

	Junonia oenone	LC
	Junonia rhadama	NA
	Precis eurodoce	NA
	Hypolimnas misippus	NA
	Cyrestis camillus elegans	NA
	Sevenia howensis	NA
	Pseudoacraea imerina	NA
	Neptis kikideli	NA
	Aterica rabena	NA
	Acraea ranavalona	NA
	Acraea dammii	NA
	Acraea igati	NA
	Phalanta phalanta aethiopica	NA
	Phalanta madagascariensis	NA
Hesperiidae:	*Tagiades insularis*	NA
	Eagris sabadius	NA
	Fulda coroller	NA
	Fulda rhadama	NA
	Acleros leucopyga	NA
	Borbo havei	NA

Table 6e. Odonata (Dragonflies and Damselflies)

Dragonfly and damselfly species occupying the littoral habitats of Sainte Luce. Species inventory based on the foundational work of Schütte & Razafindraibe (2007), with additional species observed since 2015 by SHR (verified by Kai Schütte).

Order	Family	Species	IUCN Status
Odonata	Calopterygidae	*Phaon iridipennis*	LC
	Megapodagrionidae	*Nesolestes* sp.1	
		Nesolestes sp.2	
		Protolestes kerckhoffae	DD
	Coenagrionidae	*Azuragrion kauderni*	LC
		Ischnura senegalensis	LC
		Ceriagrion glabrum	LC
		Ceriagrion nigrolineatum	LC
		Pseudagrion cf. *tinctipenne*	DD
		Teinobasis alluaudi	EN
	Platycnemididae	*Paracnemis alluaudi*	LC
		Platycnemis sp.	
	Aeshnidae	*Anax tumorifer*	LC
		Gynacantha malgassica	DD
	Gomphidae	*Isomma* sp. nov	
	Corduliidae	*Hemicordulia similis*	LC
		Nesocordulia malgassica	DD
		Nesocordulia mascarencia	DD
	Libellulidae	*Calophlebia karschi*	DD
		Neodythemis fitzgeraldi	LC
		Hemistigma affine	LC
		Orthetrum abbotti	LC
		Orthetrum azureum	LC
		Orthetrum icteromelas	LC
		Orthetrum lemur	LC
		Thermorthemis madagascariensis	LC
		Acisoma cf. *ascalaphoides*	EN
		Diplacodes exilis	LC
		Diplacodes lefebvrii	LC
		Trithemis sp.	
		Palpopleura vestita	LC
		Rhyothemis cognata	LC
		Pantala flavescens	LC
		Tramea limbata	LC
		Tholymis tillarga	LC
		Urothemis assignata	LC
		Libellulosoma minuta	DD